THE GENETICS OF FLOWERING TIME IN *RAPHANUS SATIVUS* L. CV. 'CHINESE DAIKON'

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By

Ahsan Ahmad Vahidy

Dissertation Committee:

Richard W. Hartmann, Chairman
James C. Gilbert
Henry Y. Nakasone
Yoneo Sagawa
Richard E. Green

We certify that we have read this dissertation and that in our opinion it is satisfactory in scope and quality as a dissertation for the degree of Ph.D. in Horticulture.

DISSERTATION COMMITTEE

Richard W. Hartmann
Chairman

James E. Gilbert

Henry Y. Nakasone

Yoneo Sagawa

R. E. Green

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INTRODUCTION

For the development of an effective plant breeding program, both the presence and identification of genetic variability are essential. The main objective of quantitative genetic studies is to estimate the magnitude of genetic variance, so that predictions about improvements due to a selection program can be made accurately. For the greatest accuracy a knowledge of the relative size of the different genetic variances is required. One of the main objectives of estimating the genetic variance is to estimate the magnitude of the heritability of that character. This enables the breeder to adopt an effective method of selection for the improvement of the crop. If the heritability is high, reliance may be placed mainly on individual plant performance. If it is low, more emphasis should be given to progeny tests and replicated trials in the breeding programs.

Phenotypic data are used to infer conclusions about the genotype. Therefore, proper understanding of phenotypic variance is necessary for appropriate interpretations of the data. The phenotype reflects non-genetic as well as genetic influences and these two are not independent. A change in environment does not necessarily cause the same phenotypic response in all genotypes; likewise, a similar genotypic variation may not produce the same phenotypic variation under different environments. This type of interplay is known as genotype-environment interaction. Plant breeders generally agree that such interactions have an important bearing on breeding programs. However, opinions differ as to how to utilize this knowledge for a better breeding program. Some

breeders place more emphasis on the "values" of the genotypes, while others consider the "final" character such as yield or quality of prime importance. One major effect of genotype-environment interaction is to reduce the correlation between phenotype and genotype, with the result that inferences become complicated. This is true whether interest is focused on plant improvement procedures or on the mechanism of inheritance.

It is probably in the field of developmental physiology that the answers to the basic causes of genotype-environment interaction are likely to be found. The analysis of these interactions, however, lies in the area of quantitative genetics. Better understanding of genotype-environment interactions will definitely prove significant in connection with plant improvement. However, it is quite likely that we may never be able to completely eliminate "unexplained" interactions.

'Chinese half long' is a cultivar of Raphanus sativus grown in Hawaii. It is locally known as Daikon and is the fourth largest vegetable crop by total acreage in the state of Hawaii (Collier et al. 1967). One of the main problems faced by the farmers in the production of Daikon is its premature flowering. This not only reduces the quality of the roots but also affects the yield considerably. Flowering in radish, like other crops, is affected by various environmental factors.

The present study was conducted to find whether there exists any genetic variance for flowering time in Daikon and to test the genetic-environment interaction. For this purpose selection in opposite directions was carried out for six generations, followed by replicated field experiments of selected lines at two locations during two seasons.

Crossing experiments involving Early and Late parental lines were also conducted in the greenhouse. This study may prove fruitful in developing a better breeding program for Chinese radish in the state of Hawaii.

REVIEW OF LITERATURE

Environmental Factors Affecting the Time of Flowering in Radish

There are several environmental factors that affect flowering in radish. Garner and Allard (1920) and (1923) observed that radish is a long day plant with flowers being formed only during long photoperiods. These results were later confirmed by other workers (Sinskaja, 1962; Banga and Smeets, 1956; Sulgin, 1964; and Krjuckov, 1963). It has been reported by Banga and Van Bennekom (1962) that flowering in radish is accelerated at higher temperatures and no flowering occurs at a temperature of 8 degrees Centigrade. However, flower formation was induced in Japanese radish by low temperature (Eguchi et al. 1963). Strong light intensity is reported to reduce the effect of long photoperiods as far as flowering in radish is concerned (Banga and Van Bennekom, 1962).

Genes that control the time of flowering have been reported in sorghum (Quinby, 1966), corn (Hallauer, 1965), cotton (Kohel et al. 1965), tomato (Honma et al. 1963), barley (Davies, 1959), pea (Rowlands, 1964), bean (Coyne, 1966), castor bean (Zimmerman, 1957), jute (Eunus and Salam, 1969) and many other crops. However, only the literature on the genetics of flowering of the bolting crops will be reviewed here.

Genetics of Time of Flowering in Bolting Crops

Allard (1919) reported that in giant tobacco plants blossoming did not normally take place when they were grown in the field. To obtain normal blossoms these plants were transplanted into the greenhouse in the fall. When crosses were made between this type and varieties which

blossomed normally, the mammoth type of flowering was found to be recessive. In the F_2 generation mammoth plants occurred in proportions approaching 25 percent, which suggested control by a single gene. Lang (1948) confirmed these results by crossing short day 'Maryland Mammoth' and day neutral 'Java'. Smith (1950) transferred the recessive mammoth gene of Nicotiana tabacum to a genotype of Nicotiana rustica by back crossing. He, too, suggested single gene inheritance of the character.

Dudok van Heel (1927) reported that bolting in sugar beet is genetically controlled. Crosses of strains with very few bolters with strains with many bolters gave progeny with few bolters. Also crosses between two strains, both with many bolters, gave a progeny with many bolters. Munerati, as cited by Owen et al. (1940), investigated an annual beet and showed that a single genetic factor was associated with a clearcut annual habit. Owen et al. (1940) identified a factor for bolting in sugar beet which they designated as B'. This is regarded as allelic to factor B discovered by Munerati and further described by Abegg (1936). Factor B' was identified by hybridizing selected parental material and testing the back cross progenies.

The inheritance of photoperiodism in lettuce has been studied by Bremer (1931) and Bremer and Grana (1935). These studies reveal that photoperiodic reaction in lettuce is inherited in a simple Mendelian manner, response to photoperiodism being dominant to lack of response. Lindqvist (1960) confirmed that the reaction to long day is dominant in the F_1 plants. F_2 data of crosses between long day and day neutral lines confirm the monohybrid inheritance of photoperiodism. However, when day neutral Lactuca sativa lines were crossed with L. serriola, a

more complicated segregation was found in the F_2. The frequency distribution was unimodal with narrower variation. Lindqvist concluded that the effect of the dominant gene is modified by other genes.

The behavior of bolting in cabbage has been investigated by Sutton (1924). The results of the crosses between bolting and hearting varieties revealed that bolting habit in cabbage was controlled by a single recessive gene.

Parlevliet (1968) believes that the genetic control of earliness in spinach, a long day plant, is most likely polygenic, although the day length requirement itself might be controlled by only a few genes.

Flowering time in three short day species of Solidago sempervirens has been studied by Goodwin (1944). After studying F_1 and F_2 generations, he concluded that at least nine genes are responsible for the control of flowering in Solidago. He assumed that these genes are located in many, if not all, of the linkage groups, as the haploid chromosome number of Solidago is nine.

Genetics of Time of Flowering in Radish

Frost (1923) found that in three out of four crosses between early and late lines of the cultivated species of radish, Raphanus sativus, the hybrids flowered "nearly or quite as early as the earlier selfed lines, and the general average was earlier." More or less similar results were obtained with crosses of the wild species, Raphanus raphanistrum, as well as with crosses involving the wild X the cultivated species. However, from the results of another planting reported in the same study, he concluded that the time of flowering was controlled by a dominant lateness gene. Probably the contradictory

results were due to the lack of a proper control. This was especially needed here because he grew the parents and the offspring at different times.

Panetsos and Baker (1968) found little variation in the period from germination to flowering in both R. sativus and R. raphanistrum. F_1 plants bloomed (both in summer and winter) earlier than those of the R. sativus parent, but later than those of R. raphanistrum. Three groups were identified among the F_2 plants, early, medium, and late in the ratio of 5 : 10 : 3.

Bidirectional Selection

There are a number of examples in the literature where selections in opposite directions have been made. Perhaps the largest experiment of this nature is from Illinois with corn of high and low oil and protein contents (Woodworth et al. 1952; Leng, 1961; and Leng, 1962). After fifty generations of selection for high and low oil and protein contents, it was reported that progress could still be made in the high oil and low protein strains, while little progress was noted in either the high protein or low oil strains in the last fifteen to twenty generations. When these four strains were subjected to thirteen generations of selection in the opposite direction they showed significant and rapid responses. The response was immediate in the high oil and high protein, but was delayed for several generations in the two low strains. A higher coefficient of variation was found in three of the four reverse selected strains than in the comparable regular forward selections. In reverse low oil, the coefficient of variation was

approximately half that of the regular low oil strain in the more recent generations of selection. When actual response and the predicted response by extrapolation of regression trend lines were compared, serious discrepancies were noted in at least nine out of twelve predictions. The selection response formulae also yield unsatisfactory predictions. The authors were unable to give a satisfactory genetic explanation for the results.

Most of the work on bidirectional selection has been done with small animals. Falconer (1953) carried out selection for both large and small size in mice for eleven years. Heritability estimated by divergence between the two lines was reported for each generation of selection. It varied from 2.0 percent (in the sixth generation) to 77.1 percent (in the eleventh generation).

Prevosti (1967) carried out selection for long and short wings in Drosophila in three pairs of lines. He found lower heritabilities in the lines selected for long wings, especially in the later generations of selection. Realized heritabilities for long wings ranged from 21 percent to 43 percent and for short wings from 31 percent to 53 percent.

Hardin and Bell (1967) conducted two-way selection in Tribolium for weight on two levels of nutrition. They have estimated heritability by sire component, dam and offspring covariances, and full sib covariances, and have calculated the realized heritabilities. Heritability estimates on the "good" ration were 21 percent when calculated from the sire component and 97 percent when calculated from the full sib covariances. Realized heritability for the same line was 31 percent for high selection and 35 percent for low selection.

Krider, et al. (1946) in selection experiments for high and low rate gain in swine, estimated intraline heritability as 17 percent and interline heritability as 25 percent. Heritability was estimated directly from the interline differences resulting from selection, and indirectly from that portion of the variance within lines and years which was due to heritable differences between sires.

Dickerson and Grimes (1947) have presented the results from selecting for high and low feed requirements per pound of gain in two strains of Duroc swine. Heritabilities, estimated from regression of progeny on mean of the parents, of feed requirements and daily gain were 26 percent and 43 percent respectively. The lower heritability of feed requirements was due to a stronger negative correlation between the dam's heritable and environmental influences on the feed requirements than on the growth rates of her pigs, as measured by regression of the progeny on the sire and dam separately.

Robertson (1955) and Falconer (1955) have reviewed the literature on bidirectional selection experiments in Drosophila and mice respectively.

Falconer (1953) has discussed the possible causes of asymmetry in bidirectional selection. He suggested possible causes as unequal gene frequencies, directional dominance, and an unsuitable scale of measurement. Furthermore, he believed that inbreeding depression is the most potent factor for exposing directional dominance.

Zucker (1960) has explored a method for carrying on computer model breeding experiments combining moderate inbreeding due to small population size with selection for high and low values of a polygenic

character subject to large nongenetic variation. He concluded that selection affects all three important consequences of small population size, viz., gene fixation, loss of heterozygosis and random genetic drift. According to him, some kind of asymmetry in two way selection is to be expected from dominant genes in small populations even under the most favorable conditions for avoiding it.

Genotype-Environment Interaction for Time of Flowering

The literature on genotype-environment interaction is very large. In the opinion of Allard and Bradshaw (1964), "Probably no one has the competence to review this literature in its entirety ...". Here, I will restrict myself to the literature pertaining to flowering time only.

Fisher (1918) was probably the first to separate genetic variance into three components: additive variance, dominance variance, and epistatic variance. Charles and Smith (1939) and Powers (1942) separated genetic from total variance by use of estimates of environmental variance based on nonsegregating populations. Robinson, Comstock, and Harvey (1949) used a method to measure heritability that involved the estimation of components of variance through the study of biparental progenies. Warner (1952) utilized two inbred lines and their F_1, F_2, and back cross progenies to estimate heritability. He found it to be 32 percent for the date of silking in corn.

Jinks (1954) has studied the flowering time in Nicotiana rustica, utilizing diallel crosses. He developed a method of analyzing the data based on partitioning of variances and covariances. The regression of array covariance on variance was expected to have a slope of one. The

data of flowering time were in agreement with this theoretical expectation.

Allard (1956) has demonstrated the use of diallel crosses to find genotype-environment interactions. Utilizing Jinks' data on eight varieties of Nicotiana rustica, he showed that the intervarietal hybrids had unimportant epistatic interaction for date of flowering. The additive genetic effects were found to be comparatively stable, but the dominance effects appeared quite unstable in different environments.

Jinks (1956) has extended the studies on the flowering of Nicotiana, using the data of F_2 and back cross generations derived from a diallel set of crosses. He found in Nicotiana rustica varieties significant differences in the genetical control of flowering time in the two seasons. These differences involved not only variation in the magnitude of the components of variation but also the presence of duplicate gene interactions in one of the two seasons. Also, linkage involving at least four factors was detected in one of the two seasons.

Perkins and Jinks (1968 a) have shown that a significant proportion of the genotype-environment interaction component of variation is a linear function of the additive environmental component. However, quite often there is a significant remainder that is non-linear. In another report (1968 b) the nature of the non-linear component of variation was studied by separating the lines into groups on the basis of significant positive and negative correlations for deviations from the linear regression. A reduction in the non-linear portion of the variation due to genotype-environment interaction was observed from

grouping the lines. However, a significiant non-linear portion of interaction was left even after grouping.

Lindsey, et al. (1962) utilized half sib families of two open pollinated varieties of corn. The experiments were conducted at two locations in two years. A meaningless negative value was found for the dominance variance for the date of flowering in the first planting. New half-sib families were made for the second planting. The dominance variance, though still negative, was much higher for the date of flowering for this planting. The authors hypothesized that the meaningless negative value for dominance variance might have been due to a high degree of assortative mating, since individual plants would be more likely to mate with others which flowered at the same time. The degree of assortative mating was apparently somewhat reduced in the second planting.

Goodman (1965) utilized full-sib and half-sib families of Corn Belt Composite and West Indian Composite corn grown in Iowa and North Carolina. The estimates of genotypic variance, additive genetic variance, and the interactions of these two factors with location were higher in West Indian Composite than in the Corn Belt Composite.

da Silva and Lonnquist (1968) used Robinson and Comstock's Design I to study differences in genetic variances for flowering time in two populations, resulting from two selection systems in corn. The population developed from one selection system had a significant Female X Year interaction variance for flowering time. The variance components due to Males and Females in Males were significant in both populations.

Liang and Walter (1968) worked with three crosses of grain sorghum. They evaluated the parental lines and their F_1, F_2 and back crosses. They were able to partition epistatic variance into additive x additive epistatic, additive x dominance epistatic, and dominance x dominance epistatic effects for the half blooming day. F-tests showed that the dominance x dominance variance was significant in all three crosses, the additive x dominance variance was significant in one cross, and the additive x additive variance was significant in two crosses. From these results they concluded that Genetic models assuming negligible epistasis may be somewhat biased.

Environmentally Induced Heritable Changes in Time of Flowering

The issue of genotype-environment interaction has become more complicated with the discovery of environmentally-induced heritable changes (transmutations). Hill (1965, 1967), and Hill and Perkins (1969) have reported transmutation of flowering time in an inbred variety of Nicotiana rustica. This variety was treated with all the eight possible combinations of presence or absence of Nitrogen, Phosphorus, and Potassium fertilizers. The progeny of these eight treatment lines differed in mean flowering time, even after five generations of selfing. The plants of a particular generation were treated alike after the initial treatment. It was found that the differences in the flowering time were mainly due to Potassium treatment. The variance due to selected vs. unselected lines for early flowering was found to be highly significant. This further suggested that the change (transmutation) was heritable. The variance due to selected vs.

unselected lines for late flowering was nonsignificant. However, the variance due to selected vs. unselected x environment interaction was highly significant, and this probably masked the response to selection for lateness.

MATERIALS AND METHODS

Selection Experiments

The type of radish known in Hawaii as Chinese Daikon is grown from seeds saved by the farmers from each crop. Such seed was obtained to undertake the present study. In 1964 seedlings grown in the greenhouse were treated with 1.0 percent, 0.2 percent, and 0.1 percent concentrations of colchicine. A number of plants, particularly those treated with the higher concentrations of colchicine, died. Plants were numbered 1 to 49; of which 1 to 16 were those treated with 1.0 percent concentration, while 17 to 32 and 33 to 49 were those treated with 0.2 percent and 0.1 percent concentrations respectively.

For the present studies seeds of selected colchicine-treated plants together with seeds of untreated plants were grown in the field for selection for late flowering. In all the field plantings the usual cultural practices were employed unless otherwise mentioned.

Each plot was a row 25 feet long, spaced 4 feet apart. Seeds were hand sown and thinned 3 or 4 weeks later about one foot apart. Furrow irrigation was applied when necessary. Fertilizers were applied according to the recommendation for the particular location. Weeding was either by hand or by the use of recommended herbicides.

Flowering date was recorded as the day when floral buds were just visible. Data were collected every 2 to 4 days in the fields and daily in the greenhouse.

Selected plants were covered with net cloth after pod set to avoid damage by birds. At maturity the pods were harvested and dried either under the sun or indoors at room temperature. Individual plant

selection from open pollinated plants was used, except in one generation where selected plants within lines were bulked.

Plantings were conducted in the fields at the University of Hawaii, Manoa campus, at the Poamoho and Waimanalo Experimental Farms, and in the greenhouse. Poamoho Experimental Farm is located about 30 miles North of the University campus, at 700 feet above sea level with a Wahiawa soil type, which is a low humic latosol soil. The mean maximum and minimum temperatures for the year 1968-69 were 80.9 and 66.8 degrees Fahrenheit. The annual rainfall is 37.5 inches. Waimanalo Experimental Farm is situated about 20 miles East of the campus, at 50 feet above sea level with a Waimanalo soil type, which is a gray hydromorphic soil. For 1968-69 the mean maximum and minimum temperatures were 82.1 and 71.4 degrees Fahrenheit. The annual rainfall is 45.1 inches.

In the summer of 1966 a planting was made consisting of untreated seeds and colchicine treated seeds which had been selected for late flowering for 0, 1, and 2 generations. Size of stomata, guard cells and pollen grains were studied to attempt to identify tetraploids. However, no differences between the check and the treated (selected or unselected) plants were found.

At this time selection was started for earliness in flowering, and selection for lateness was continued. The data of these selection experiments were used to compute the realized heritability of mean flowering time, using the following formula:

$G_s = k \times St.Dev. \times h^2$

where G_s = genetic advance under selection,

k = constant for particular selection pressure,

St.Dev. = phenotypic standard deviation, and

h^2 = realized heritability.

After four generations of selection for late flowering an experiment was planned to test whether genetic variability still existed in these lines. For this purpose, selection in the opposite direction (i.e., for earliness) was initiated in 25 breeding lines that had been selected for late flowering for four generations. Selection for late flowering was also continued.

Data from the fourth and fifth generations of selection for lateness and the first generation of selection for earliness have been used to estimate realized heritabilities for the various lines. As the parental generation and the offspring were grown at different times, the flowering dates of the parental generation were transformed to make them comparable to that of the progeny. This transformation was based on the assumption that breeding lines number 13 and 18 are homozygous, since there was no response to selection in either direction in these lines. The original and transformed parental means, and the means of their early and late selected progeny are given in Table 1. The method of transformation is described in Table 2. For each transformed parental mean, the phenotypic standard deviation was calculated from the coefficient of variation of the untransformed mean in the following manner:

Table 1. Mean Flowering Days of Parental, Early Selected and Late Selected Lines

Line No.	Original Parent[a]	Progeny		Transformed Parent[d]
		Early Selection[b]	Late Selection[c]	
1	90.31	54.12	68.82	67.08
2	78.60	52.53	66.68	58.38
3	78.60	62.30	75.16	58.38
4	81.74	57.50	74.57	60.71
5	81.74	57.31	67.25	60.71
6	85.09	62.66	74.54	63.20
7	88.30	50.23	68.50	65.58
8	88.30	56.19	74.40	65.58
9	88.30	52.34	77.78	65.58
10	88.50	57.73	72.00	65.73
11	90.37	66.31	69.79	67.12
12	83.50	57.25	62.89	62.02
13	82.34	62.00	60.16	61.16
14	90.70	62.30	72.45	67.37
15	74.75	53.00	68.17	55.52
16	84.42	45.81	64.33	62.70
17	84.42	66.00	72.19	62.70
18	91.52	67.40	68.73	67.97
19	91.80	57.42	69.03	68.18
20	91.80	66.45	71.80	68.18
21	85.34	61.80	66.39	63.38
22	81.00	57.60	62.60	60.16
23	85.20	63.95	69.61	63.28
24	85.20	62.73	70.09	63.28
25	80.31	51.45	62.60	59.65

[a] 4th generation of late selection. Poamoho--Fall, 1967 planting.
[b] Selection in opposite direction. Poamoho--Summer, 1968 planting.
[c] 5th generation of late selection. Poamoho--Summer, 1968 planting.
[d] Transformation is applied to make the figures of parental lines comparable to those of progeny lines. See Table 2 for procedure.

Table 2. Transformation of Parental Lines in Table 1

Line No.[a]	Fall--1967 Planting	Summer--1968 Planting	
	Original Parental Line	Early Selection	Late Selection
13	82.34	60.16	62.00
18	91.52	68.73	67.40
Total	173.86	128.89	129.40
Mean	86.93	64.44	64.70
Total	86.93	129.14	
Mean	86.93	64.57	

Transformation: 86.93 days to flowering of Fall--1967 planting is equal to 64.57 days to flowering of Summer--1968 planting. The data of original parental line of Table 1 is transformed on this scale.

[a]These are considered homozygous lines on the basis of their performance. See Table 1.

Original mean = 79.12

Original standard deviation = 9.94

Original coefficient of variation = $\frac{9.94}{79.02} \times 100 = 12.59$

Transformed mean = 59.11

Transformed standard deviation = $\frac{12.59 \times 59.11}{100} = 7.44$

Main Field Experiment

To study genotype-environment interactions 10 early flowering, 2 check and 10 late flowering lines were selected. These lines were labelled as E-1 to E-10 for early flowering lines, Ck-1 and Ck-2 for check lines, and L-1 to L-10 for late flowering lines. Pedigrees of these lines are given in Table 3.

These 22 lines were grown in a Randomized Complete Block Design, with 4 replications at two farms, during two times of year. Independent randomization was done for each of the four plantings. Replications, farms, and times of year are considered as random effects while the breeding lines are as fixed effect.

The two farms were Poamoho and Waimanalo Experimental Farms, while the two times of the year were Fall of 1968 (October 1968 to January 1969) and Spring of 1969 (February 1969 to May 1969). The average maximum and minimum temperatures during the Fall, 1968 period were 79.8 and 66.1 degrees Fahrenheit at Poamoho, and 81.6 and 69.7 degrees Fahrenheit at Waimanalo Experimental Farms. The average maximum and minimum temperatures during the spring, 1969 period were 77.1 and 64.7 degrees Fahrenheit at Poamoho, and 78.9 and 69.6 degrees Fahrenheit at Waimanalo. The rainfall during these periods was 37.17 inches at

Table 3. Pedigrees of Lines Referred to in Tables 4 to 11

Line Number	Pedigree	Group of Lines
E-1	U[a]-100-E[b]-5-1-3-B[c]	Early group 1
E-2	U-100-E-5-1-6-B	
E-3	U-100-E-5-2-1-B	
E-4	U-100-E-5-2-2-B	
E-5	C[d]-25-L[b]-7-E-2-1-3-B	Early group 2
E-6	C-25-L-7-E-2-1-5-B	
E-7	C-25-L-8-E-2-4-4-B	
E-8	C-25-L-11-E-4-1-1-B	
E-9	C-26-L-8-2-E-1-2-1-B	Early group 3
E-10	C-26-L-8-2-E-1-2-2-B	
Ck-1	unselected original seeds	Check group
Ck-2	unselected original seeds	
L-1	C-30-L-5-3-1-3-2-B	Late group 1
L-2	C-30-L-5-3-5-3-2-B	
L-3	C-30-L-5-3-5-4-1-B	
L-4	C-30-L-5-3-5-5-1-B	
L-9	C-30-L-5-3-1-1-2-B	
L-10	C-30-L-5-3-5-3-4-B	
L-5	C-31-L-3-3-5-1-1-B	Late group 2
L-6	C-31-L-3-3-5-3-2-B	
L-7	C-33-L-4-2-3-1-1-B	Late group 3
L-8	C-42-L-5-4-4-3-2-B	Late group 4

[a]Not treated with colchicine.
[b]Early or late selection in generations following the symbol.
[c]Seeds of the selected plants bulked within line.
[d]Colchicine treated.

Poamoho, Fall; 37.32 inches at Waimanalo, Fall; 9.46 inches at Poamoho, Spring; and 12.93 inches at Waimanalo, Spring. From these figures it can be seen that Waimanalo was generally somewhat warmer, but there was little difference in rainfall.

The dates when 50 percent of the plants had flowered at Poamoho-Fall, Poamoho-Spring, Waimanalo-Fall, and Waimanalo-Spring are given in Tables 4, 5, 6, and 7. For analyses of variance the lines were grouped in 4 ways, namely, 10 Early vs. 10 Late Lines; 3 Early vs. 1 Check vs. 4 Late groups of lines; 1 Check vs. 3 Early groups of lines; and 1 Check vs. 4 Late groups of lines. The three Early groups were made on the basis of whether they had been selected for lateness for 0, 1, or 2 generations, while the grouping of Late lines was based on their origin tracing back to a single seed (see Table 3). For the analyses of groups of lines, the data used were the mean 50 percent flowering day of lines in each particular group.

For each of the four types of groupings the heterogeneity of the error variances of the four plantings was tested by Bartlett's test of heterogeneity. The Chi-square had significantly large values for all the four types of analyses and therefore, the data of the four plantings could not be pooled.

It was possible to obtain homogeneous error variances by utilizing the following method of transformation. The mean 100 percent flowering day of the two Check lines (four replications each) was computed for each planting. The individual flowering dates were then expressed as percentages of the mean 100 percent flowering day of the Check lines.

Table 4. Days to 50 Percent Flowering; Poamoho--Fall, 1968

Breeding Line	Replication			
	I	II	III	IV
E-1	50	45	47	48
E-2	47	47	45	48
E-3	44	48	47	46
E-4	43	46	47	46
E-5	47	47	47	45
E-6	45	47	48	46
E-7	47	47	47	47
E-8	49	51	48	48
E-9	49	47	50	47
E-10	48	49	47	49
Ck-1	62	65	58	59
Ck-2	62	65	61	62
L-1	81	81	78	78
L-2	78	77	79	76
L-3	80	79	77	75
L-4	77	83	79	82
L-5	79	78	82	78
L-6	80	77	81	76
L-7	79	80	81	81
L-8	85	85	83	81
L-9	81	78	80	78
L-10	77	81	79	81

Table 5. Days to 50 Percent Flowering; Poamoho--Spring, 1969

Breeding Line	Replication			
	I	II	III	IV
E-1	37	36	37	38
E-2	34	35	35	35
E-3	36	34	37	36
E-4	35	36	35	36
E-5	35	36	36	36
E-6	35	36	35	35
E-7	38	38	37	39
E-8	36	37	35	37
E-9	37	36	38	38
E-10	37	38	36	38
Ck-1	46	45	44	42
Ck-2	44	45	46	45
L-1	57	55	55	59
L-2	59	61	58	57
L-3	58	58	56	57
L-4	59	60	58	58
L-5	56	57	57	56
L-6	57	57	57	57
L-7	58	57	58	58
L-8	59	59	59	59
L-9	57	59	60	57
L-10	59	57	57	56

Table 6. Days to 50 Percent Flowering; Waimanalo--Fall, 1968

Breeding Line	Replication			
	I	II	III	IV
E-1	52	52	50	55
E-2	52	52	52	51
E-3	53	50	51	51
E-4	51	51	50	49
E-5	51	51	53	51
E-6	51	56	53	52
E-7	57	51	50	49
E-8	55	58	55	54
E-9	59	56	52	51
E-10	53	54	55	53
Ck-1	63	64	61	63
Ck-2	68	71	62	61
L-1	88	91	89	91
L-2	82	81	89	88
L-3	84	86	87	88
L-4	91	85	86	90
L-5	90	86	87	90
L-6	88	87	88	85
L-7	85	90	90	90
L-8	90	89	90	91
L-9	89	89	90	88
L-10	89	89	89	91

Table 7. Days to 50 Percent Flowering;
Waimanalo--Spring, 1969

Breeding Line	Replication			
	I	II	III	IV
E-1	36	37	37	39
E-2	38	37	37	38
E-3	37	38	37	38
E-4	37	37	37	36
E-5	37	37	37	38
E-6	37	38	38	36
E-7	38	38	38	38
E-8	38	37	40	37
E-9	40	39	37	39
E-10	37	38	38	37
Ck-1	50	49	49	49
Ck-2	49	50	51	50
L-1	63	63	66	65
L-2	66	67	67	67
L-3	66	64	68	68
L-4	70	61	67	68
L-5	60	65	66	64
L-6	66	65	66	67
L-7	70	66	67	68
L-8	69	66	66	66
L-9	64	68	66	66
L-10	64	67	67	66

The transformed data for the four plantings are given in Tables 8 to 11. Transformed data were analyzed separately for each planting. The form of analysis of variance for an individual planting is given in Table 12.

The method employed to test the heterogeneity of error variances is described in Table 26. The sources of variation and degrees of freedom for the combined analysis of variance for four plantings are given in Table 13. The expectations of mean squares for each source of variation are given in Figure 1. Figure 2 gives the formulas for calculation of the various components of variance from the calculated mean squares. These components of variance are obtained through simple algebric manipulation of the expectations of mean square.

F-tests for main effects as well as for interaction effects are described at the bottom of Table 32, except the F-test for breeding lines effect. This test was done as suggested by Cochran and Cox (1955), and is explained in Table 14.

Estimates of heritabilities of mean flowering time of Check lines were possible by assuming certain late flowering lines (L-2, L-3, L-6, L-7, and L-10) to be homozygous. These lines were selected at random from those Late lines that had rather low coefficients of variation (see Tables 15 to 18). Since the variance of flowering time increases with an increase in mean flowering time even though the relative variability is the same, the coefficient of variation, rather than the variance, was used for comparison of lines with different means. The following method was employed to estimate the heritability of the Check lines:

Table 8. Transformed Data for 50 Percent Flowering; Poamoho--Fall, 1968[a]

Breeding Line	Replication			
	I	II	III	IV
E-1	66.01	59.40	62.04	63.36
E-2	62.04	62.04	59.40	63.36
E-3	58.08	63.36	62.04	60.72
E-4	56.76	60.72	62.04	60.72
E-5	62.04	62.04	62.04	59.40
E-6	59.40	62.04	63.36	60.72
E-7	62.04	62.04	62.04	62.04
E-8	64.68	67.33	63.36	63.36
E-9	64.68	62.04	66.01	62.04
E-10	63.36	64.68	62.04	64.68
Ck-1	81.85	85.81	76.57	77.89
Ck-2	81.85	85.81	80.53	81.85
L-1	106.93	106.93	102.97	102.97
L-2	102.97	101.65	104.29	100.33
L-3	105.61	104.29	101.65	99.01
L-4	101.65	109.57	104.29	108.25
L-5	104.29	102.97	108.25	102.97
L-6	105.61	101.65	106.93	100.33
L-7	104.29	105.61	106.93	106.93
L-8	112.21	112.21	109.57	106.93
L-9	106.93	102.97	105.61	102.97
L-10	101.65	106.93	104.29	106.93

[a]See text for method of transformation.

Table 9. Transformed Data for 50 Percent Flowering; Poamoho--Spring, 1969[a]

Breeding Line	Replication			
	I	II	III	IV
E-1	66.37	64.57	66.37	68.16
E-2	60.99	62.78	62.78	72.78
E-3	64.57	60.99	66.37	64.57
E-4	62.78	64.57	62.78	64.57
E-5	62.78	64.57	64.57	64.57
E-6	62.78	64.57	62.78	62.78
E-7	68.16	68.16	66.37	69.95
E-8	64.57	66.37	62.78	66.37
E-9	66.37	64.57	68.16	68.16
E-10	66.37	68.16	64.57	68.16
Ck-1	82.51	80.72	78.92	75.34
Ck-2	78.92	80.72	82.51	80.72
L-1	102.24	98.65	98.65	105.83
L-2	105.83	109.42	104.03	102.24
L-3	104.03	104.03	100.45	102.24
L-4	105.83	107.62	104.03	104.03
L-5	100.45	102.24	102.24	100.45
L-6	102.24	102.24	102.24	102.24
L-7	104.03	102.24	104.03	104.03
L-8	105.83	105.83	105.83	105.83
L-9	102.24	105.83	107.62	102.24
L-10	105.83	102.24	102.24	100.45

[a]See text for method of transformation.

Table 10. Transformed Data for 50 Percent Flowering; Waimanalo--Fall, 1968[a]

Breeding Line	Replication			
	I	II	III	IV
E-1	62.84	62.84	60.42	66.46
E-2	62.84	62.84	62.84	61.63
E-3	64.05	60.42	61.63	61.63
E-4	61.63	61.63	60.42	59.21
E-5	61.63	61.63	64.05	61.63
E-6	61.63	67.67	64.05	62.84
E-7	68.88	61.63	60.42	59.21
E-8	66.46	70.09	66.46	65.25
E-9	71.30	67.67	62.84	61.63
E-10	64.05	65.25	66.46	64.05
Ck-1	76.13	77.34	73.71	76.13
Ck-2	82.17	85.80	74.92	73.71
L-1	106.34	109.96	107.55	109.96
L-2	99.09	97.88	107.55	106.34
L-3	101.51	103.92	105.13	106.34
L-4	109.96	102.71	103.92	108.76
L-5	108.76	103.92	105.13	108.76
L-6	106.34	105.13	106.34	102.71
L-7	102.71	108.76	108.76	108.76
L-8	108.76	107.55	108.76	109.96
L-9	107.55	107.55	108.76	106.34
L-10	107.55	107.55	107.55	109.96

[a]See text for method of transformation.

Table 11. Transformed Data for 50 Percent Flowering; Waimanalo--Spring, 1969[a]

Breeding Line	Replication			
	I	II	III	IV
E-1	59.14	60.78	60.78	64.07
E-2	62.42	60.78	60.78	62.42
E-3	60.78	62.42	60.78	62.42
E-4	60.78	60.78	60.78	59.14
E-5	60.78	60.78	60.78	62.42
E-6	60.78	62.42	62.42	59.14
E-7	62.42	62.42	62.42	62.42
E-8	62.42	60.78	65.71	60.78
E-9	65.71	64.07	60.78	64.07
E-10	60.78	62.42	62.42	60.78
Ck-1	82.14	80.49	80.49	80.49
Ck-2	80.49	82.14	83.78	82.14
L-1	103.49	103.49	108.42	106.78
L-2	108.42	110.06	110.06	110.06
L-3	108.42	105.13	111.70	111.70
L-4	114.99	100.20	110.06	111.70
L-5	98.56	106.78	108.42	105.13
L-6	108.42	106.78	108.42	110.06
L-7	114.99	108.42	110.06	111.70
L-8	113.55	108.42	108.42	108.42
L-9	105.13	111.70	108.42	108.42
L-10	105.13	110.06	110.06	108.42

[a]See text for method of transformation.

Table 12. Form of Analysis of Variance for Individual Planting

Source of Variation	df	Expectations of Mean Square
Replication (R)	(r-1)	$\sigma^2 + b\sigma^2_R$
Breeding Lines (B)	(b-1)	$\sigma^2 + r\sigma^2_B$
Error	(r-1) (b-1)	σ^2
Total	(rb)-1	

r = number of replications.
b = number of breeding lines.
σ^2 = error variance
σ^2_R = component of variance due to replication.
σ^2_B = component of variance due to breeding lines.

Table 13. Sources of Variation and Degrees of Freedom for Combined Analysis of Variance

Source of Variation	Degrees of Freedom
Farms (F)	(f-1)
Time (T)	(t-1)
F x T	(f-1) (t-1)
Error (a)	(tf) (r-1)
Replication over Experiments (R)	(rft)-1
Breeding Line (B)	(b-1)
B x F	(b-1) (f-1)
B x T	(b-1) (t-1)
B x T x F	(b-1) (t-1) (f-1)
Error (b)	(tf) (r-1) (b-1)
Total	(rbtf)-1

f = number of farms.
t = number of times of year.
r = number of replications per experiment.
b = number of breeding lines.

Figure 1. Sources of Variation and Expectations of Mean Square for the Combined Analysis of Variance

SOURCE OF VARIATION	CALCULATED MEAN SQUARE	EXPECTATIONS OF MEAN SQUARE
Farms (F)	M_1	$\sigma^2 + b\sigma^2_R + r\sigma^2_{BFT} + rt\sigma^2_{BF} + rb\sigma^2_{FT} + rbt\sigma^2_F$
Times of year (T)	M_2	$\sigma^2 + b\sigma^2_R + r\sigma^2_{BFT} + rf\sigma^2_{BT} + rb\sigma^2_{FT} + rbf\sigma^2_T$
F × T	M_3	$\sigma^2 + b\sigma^2_R + r\sigma^2_{BFT} + rb\sigma^2_{FT}$
Breeding lines (B)	M_4	$\sigma^2 + r\sigma^2_{BFT} + rt\sigma^2_{BF} + rf\sigma^2_{BT} + rtf\sigma^2_B$
B × F	M_5	$\sigma^2 + r\sigma^2_{BFT} + rt\sigma^2_{BF}$
B × T	M_6	$\sigma^2 + r\sigma^2_{BFT} + rf\sigma^2_{BT}$
B × F × T	M_7	$\sigma^2 + r\sigma^2_{BFT}$
Reps. in F & T	M_8	$\sigma^2 + b\sigma^2_R$
B × reps. in F & T	M_9	σ^2

σ^2 = Error Variance

σ^2_R = Component of Variance due to replications in F & T

σ^2_F = Component of Variance due to farms

σ^2_T = Component of Variance due to times of year

σ^2_B = Component of Variance due to breeding lines

σ^2_{FT} = Interaction Variance of farm effects with times of year

σ^2_{BF} = Interaction Variance of breeding lines effects with farms

σ^2_{BT} = Interaction Variance of breeding lines effects with times of year

σ^2_{BFT} = Second order interaction variance of breeding line effects with farms & times of year

b,r,t,f = Number of breeding lines, replications, times of year, farms respectively

Figure 2. Formulas to Calculate Variance Components from the Expectations of Mean Square

$$\sigma^2_{BFT} = (M_7 - M_9)/r$$

$$\sigma^2_{BT} = (M_6 - M_7)/rf$$

$$\sigma^2_{BF} = (M_5 - M_7)/rt$$

$$\sigma^2_{B} = \left[(M_4 + M_9) - (M_7 + M_8)\right]/rtf$$

$$\sigma^2_{FT} = \left[(M_3 + M_9) - (M_7 + M_8)\right]/rb$$

$$\sigma^2_{T} = \left[(M_2 + M_7) - (M_3 + M_6)\right]/rbf$$

$$\sigma^2_{F} = \left[(M_1 + M_7) - (M_3 + M_5)\right]/rbt$$

Table 14. Method for Testing Significance of Lines as in Table 32[a]

Constructed F:

$$F' = \frac{M.S._B + M.S._{BFT}}{M.S._{BF} + M.S._{BT}}$$

where $M.S._B$, etc. = Mean square for breeding lines, etc.

Constructed df:

$$df_1 = \frac{(M.S._B + M.S._{BFT})^2}{\frac{(M.S._B)^2}{df_B} + \frac{(M.S._{BFT})^2}{df_{BFT}}}$$

$$df_2 = \frac{(M.S._{BF} + M.S._{BT})^2}{\frac{(M.S._{BF})^2}{df_{BF}} + \frac{(M.S._{BT})^2}{df_{BT}}}$$

where df_B, etc. = Degrees of freedom associated with breeding lines, etc.

F' is tested for df_1 and df_2.

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[a]Based on F' test of Cochran and Cox (1955).

Table 15. Variance, Standard Deviation, Mean, and Coefficient of Variation of Flowering Time; Poamoho-Fall, 1968

Line	Variance	Standard Deviation	Mean	Coefficient of Variation in %
E-1	24.09	4.91	47.25	10.39
E-2	23.14	4.81	46.95	10.24
E-3	25.77	5.07	46.79	10.83
E-4	25.59	5.06	45.66	11.08
E-5	20.36	4.51	46.48	9.70
E-6	24.05	4.90	46.48	10.54
E-7	24.52	4.95	47.46	10.42
E-8	24.79	4.98	49.00	10.16
E-9	26.32	5.13	48.43	10.59
E-10	22.61	4.76	47.88	9.94
Ck-1	44.06	6.64	61.90	10.72
Ck-2	47.67	6.90	61.97	11.13
L-1	57.86	7.61	78.31	9.71
L-2	55.65	7.47	76.69	9.72
L-3	48.27	6.95	77.77	8.93
L-4	68.97	8.30	80.07	10.36
L-5	47.04	6.86	79.28	8.65
L-6	38.52	6.21	77.78	7.98
L-7	48.57	6.97	80.87	8.61
L-8	51.25	7.16	83.89	8.53
L-9	114.10	10.68	79.24	13.47
L-10	40.75	6.38	80.66	7.90

Table 16. Variance, Standard Deviation, Mean, and Coefficient of Variation of Flowering Time; Poamoho--Spring, 1969

Line	Variance	Standard Deviation	Mean	Coefficient of Variation in %
E-1	24.97	5.00	36.04	13.87
E-2	33.63	5.80	33.48	17.32
E-3	29.03	5.39	35.08	15.36
E-4	29.58	5.44	33.99	16.00
E-5	28.51	5.34	34.87	15.31
E-6	32.56	5.71	33.61	16.98
E-7	19.33	4.40	37.36	11.77
E-8	28.17	5.31	35.34	15.02
E-9	16.81	4.11	37.04	11.09
E-10	23.93	4.89	36.72	13.31
Ck-1	28.72	5.36	44.61	12.01
Ck-2	28.21	5.31	45.23	11.73
L-1	29.92	5.47	56.35	9.70
L-2	33.34	5.77	58.97	9.78
L-3	24.32	4.93	56.96	8.65
L-4	47.93	6.92	59.46	11.63
L-5	30.54	5.53	56.73	9.74
L-6	25.61	5.16	56.98	9.05
L-7	32.74	5.72	58.11	9.84
L-8	49.01	7.00	60.08	11.65
L-9	25.03	5.00	58.24	8.58
L-10	31.75	5.63	57.85	9.73

Table 17. Variance, Standard Deviation, Mean, and Coefficient of Variation of Flowering Time; Waimanalo--Fall, 1968

Line	Variance	Standard Deviation	Mean	Coefficient of Variation in %
E-1	29.74	5.45	52.15	10.45
E-2	20.55	4.53	51.98	8.71
E-3	18.60	4.32	52.06	8.29
E-4	20.26	4.50	50.39	8.93
E-5	29.01	5.39	52.54	10.25
E-6	37.52	6.13	54.27	11.29
E-7	39.06	6.25	52.45	11.91
E-8	42.62	6.53	55.69	11.72
E-9	35.51	5.96	54.99	10.83
E-10	35.39	5.95	54.38	10.94
Ck-1	71.95	8.48	64.65	13.11
Ck-2	70.01	8.37	66.59	12.56
L-1	76.73	8.76	88.95	9.84
L-2	85.54	9.25	85.20	10.85
L-3	43.80	6.62	85.54	7.73
L-4	71.95	8.48	87.71	9.66
L-5	69.67	8.35	87.85	9.50
L-6	37.63	6.13	86.79	7.06
L-7	47.09	6.86	89.14	7.69
L-8	53.18	7.29	89.50	8.14
L-9	46.94	6.85	89.79	7.62
L-10	43.69	6.61	90.38	7.31

Table 18. Variance, Standard Deviation, Mean, and Coefficient of Variation of Flowering Time; Waimanalo--Spring, 1969

Line	Variance	Standard Deviation	Mean	Coefficient of Variation in %
E-1	26.91	5.19	36.91	14.06
E-2	21.09	5.57	36.93	15.08
E-3	30.13	5.49	37.57	14.61
E-4	24.64	4.96	35.68	13.90
E-5	32.86	5.73	36.34	15.76
E-6	34.31	5.86	36.32	16.13
E-7	21.07	4.59	38.90	11.79
E-8	34.95	5.91	37.53	15.74
E-9	25.05	5.01	38.65	12.96
E-10	29.76	5.45	37.44	14.55
Ck-1	32.97	5.74	49.06	11.69
Ck-2	31.68	5.63	49.79	11.30
L-1	36.46	6.04	64.47	9.36
L-2	42.07	6.49	67.71	9.58
L-3	35.70	5.98	67.10	8.91
L-4	58.23	7.63	66.98	11.39
L-5	51.48	7.17	64.65	11.09
L-6	33.61	5.80	66.10	8.77
L-7	44.37	6.66	68.86	9.67
L-8	36.12	6.01	67.39	8.91
L-9	45.32	6.73	66.71	10.08
L-10	41.09	6.41	66.67	9.61

Phenotypic variance of Check line = 45.86 (mean variance of 2 Check lines, see Table 15).

Environmental variance of Check line:

Coefficient of variation of L-2 = .0972 (Table 15).

Assumption: Coefficient of variation of Check line due to environment would also be .0972.

Mean of Check line = 61.93 (mean of 2 Check lines, see Table 15).

Calculated variance of Check line due to environment = $(61.93 \times .0972)^2 = 36.04$.

Genotypic variance of Check line = 45.86 - 36.04 = 9.82.

Heritability of Check line = 9.82 / 45.86 = 21.41 percent.

Crossing Experiments

Crosses between early flowering lines and late flowering lines were made in the greenhouse in the spring of 1968. Twenty-five Early and 25 Late lines were sown in the greenhouse and, of these, 10 Early and 10 Late lines were selected for making crosses. The pedigrees of these lines are given in Table 19. Seeds were sown in jiffy pots, 6 seeds per jiffy pot, and 2 jiffy pots per line. There was a difference of 3 weeks in sowing time of Early and Late lines, so that both may bloom at the same time. Two weeks after sowing the plants were thinned to one plant per jiffy pot and were transferred to two-gallon cans. Fertilizer (8:12:14) was applied to both Early and Late plants at the rate of two teaspoons per can on 16, 30, and 40 days after sowing. Plants were watered once or twice a day as required.

Table 19. Pedigrees of P_1 and P_2 Plants Used in Crossing Experiments

Set I:

E-I	U[a]-100-E[b]-5-1-1
E-II	U-100-E-5-1-2
E-III	U-100-E-5-3-1
E-IV	C[c]-25-L[b]-8-E-2-4-1
E-V	C-26-L-8-2-E-1-2-2
L-I	C-31-L-3-3-5-3-1
L-II	C-26-L-1-6-3-3-1
L-III	C-30-L-5-3-1-1-1
L-IV	C-31-L-3-3-4-3-1
L-V	C-31-L-3-3-5-1-1

Set II:

E-VI	U-75-E-5-2-1
E-VII	U-75-E-5-2-2
E-VIII	C-25-L-11-E-4-1-1
E-IX	C-26-L-8-2-E-1-2-1
E-X	C-25-L-7-E-2-1-1
L-VI	C-30-L-5-3-1-3-1
L-VII	C-26-L-7-1-1-1-1
L-VIII	C-30-L-5-3-1-1-2
L-IX	C-30-L-5-3-5-1-1
L-X	C-31-L-3-3-5-3-1

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[a]Not treated with colchicine.
[b]Early or late selection in generations following the symbol.
[c]Colchicine treated.

Five Early and five Late flowering plants that bloomed approximately at the same time constituted Set I. In the same way Set II contained 5 different Early and 5 different Late flowering plants that bloomed approximately at the same time. Within Set all the possible crosses (including reciprocal crosses and selfs) between Early's and Late's were made.

One day before the crosses were made all the open flowers were discarded. Newly opened buds and large unopened buds were carefully emasculated with forceps. Pollen was applied directly from newly opened flowers to the stigmas of emasculated flowers. Pollinated flowers were covered with small translucent paper bags closed with paper clips. Some emasculated, unpollinated flower buds were also covered similarly to check contamination. Paper bags were removed 4 to 5 days after pollination.

F_1 seeds were sown in the late summer of 1968. For each individual cross (including reciprocals) two plants were raised. One replication was grown in two-gallon cans and the other in gallon cans. The two replications were treated alike otherwise. The plants were transferred outside the greenhouse after 4 weeks. F_1 plants belonging to different sets were kept on separate benches. Selfed P_1 and P_2 seeds were also grown at the same time. The P_1 plants were destroyed by a heavy infestation of aphids, but the mean flowering day of the P_2 plants was 3 days less than in the original spring, 1968 planting. On this basis the data of the F_1 plants were transformed by adding 3 days to all the plants.

A number of F_1 plants were destroyed by strong winds and heavy rain before blooming. As a result there were too many missing values to permit analysis of the data by Robinson and Comstock's Design II. The data are therefore, presented as the mean flowering day of F_1 plants that had a common parent in the original crosses (Table 20). An individual plant is used twice in this table, once as a common female parent and a second time as a common male parent.

F_2 seeds were obtained after open pollination of F_1 plants. F_2 plants were grown in the greenhouse during May to October, 1969. In order to make back-crosses, the F_2 seeds were sown in two lots (four replications each), with one week between the two plantings. The late parents were sown about 3 weeks before the F_2 and the Early parents about two weeks after. Twenty Check seeds (no selection) were also sown with each late and early sowing. All the plants were grown in two-gallon cans.

On the basis of the performance of the Check plants and the Early and Late parents, the data of the F_2 plants were transformed to make comparable to original parental and F_1 data in the following manner. The first Check planting (sown with Late parents) flowered from June 16 to July 10, with a mean flowering date of 50.55 days. The second Check planting (sown with Early parents) flowered from August 17 to September 18, with a mean of 77.77 days. However, rather than a continuous distribution as in other plantings, there was a gap of 12 days after the 72nd day, during which no plants flowered. Possibly this was caused by painting the glass of the greenhouse. Therefore, 12 days were subtracted from all the Check plants that flowered after the 72nd day

Table 20. Mean Flowering Day of F_1 Plants[a]

Parent Plant	Used as Female		Used as Male	
	Rep. I	Rep. II	Rep. I	Rep. II
Set I:				
E-I	57.00	58.20	60.33	61.33
E-II	55.60	57.00	60.00	62.66
E-III	61.50	65.00	60.50	63.00
E-IV	63.00	58.00	64.00	64.00
E-V	58.50	62.50	54.50	55.33
L-I	58.33	64.00	62.25	59.33
L-II	61.60	68.00	57.40	60.00
L-III	59.60	60.00	57.33	60.00
L-IV	55.75	57.33	49.33	58.00
L-V	63.75	62.40	60.50	72.50
Set II:				
E-VI	59.40	61.75	61.50	64.50
E-VII	55.00	61.00	56.50	59.50
E-VIII	65.50	69.33	62.25	62.66
E-IX	63.25	72.00	60.66	61.00
E-X	62.66	65.66	60.50	61.00
L-VI	69.33	75.00	60.00	62.33
L-VII	67.50	65.75	59.60	69.00
L-VIII	59.00	55.75	63.00	66.00
L-IX	66.50	63.00	54.33	52.66
L-X	59.25	56.50	63.66	60.50

[a]Each figure is calculated from the mean of 1 to 5 plants.

and a new mean was calculated of 71.77 days. The mean of the two Check plantings was thus 61.16 days, very similar to the overall mean of all Check plantings (60.09 days).

The F_2 flowering dates were, therefore, corrected in the following manner. Those which bloomed up to July 10 (when the first Check bloomed) had 11 days added (61.16 - 50.55 = approximately 11). Those which flowered from July 11 to July 26 had 5 days added. Those which flowered from July 27 to August 16 were left unchanged. Those which flowered from August 17 (the day the first plant of the second Check planting bloomed) to September 9 (the day when the 12 days gap period was over) had 11 days subtracted (71.77 - 61.16 = approximately 11). Those which flowered after September 10 had 23 days subtracted (12 + 11). The F_2 data were analyzed after subjecting to these corrections.

RESULTS AND DISCUSSION

Selection Experiments

The response to selection was gradual with no appreciable decrease of variability even after six generations. It was not possible to estimate the actual genetic advance due to selection in each generation because of the large effect of environment on the flowering time at different times of the year and the absence of a suitable check in all plantings. However, the Early and Late lines became more and more differentiated in each generation, until, at the end of the study, there was very little overlapping in the frequency distributions of the Early and Late lines (Figures 3 and 4). At this time the Early lines had been selected for four generations and the Late lines for six generations. The unselected Check lines had a distribution that was somewhat in between the Early and the Late lines.

The data from the selection experiments were utilized to estimate realized heritabilities of mean flowering time at different stages of selection. These estimates, for the plantings where parental and offspring generations were grown at the same time, are given in Table 21. The average realized heritability of mean flowering time was 37.42 percent. These estimates were based on the assumption that the mean performance of parents and their half sibs is same. This assumption was necessary because the offsprings were grown with the half sibs of their parents, not with their actual parents. Inclusion of the half sibs of the parents in the offspring generation was done so that comparisons between parents and offspring could be made within one planting. The environmental changes caused erratic changes in the time

Figure 3. Cumulative Percentage of Flowering for the Early, Check, and Late Populations in the Two Plantings of Fall, 1968

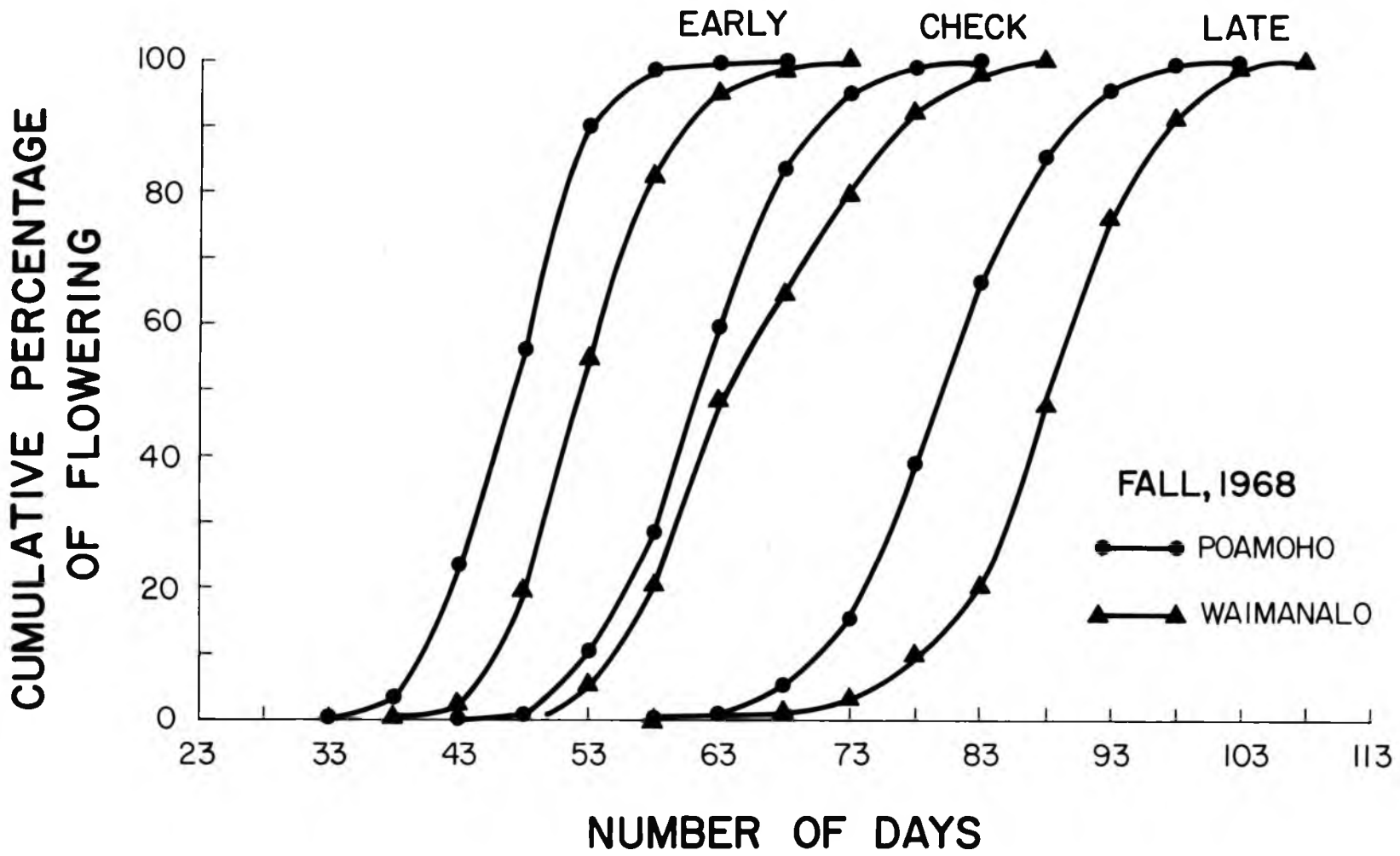

EARLY
CHECK
LATE
100
80
60
40
20
0
23
33
43
53
63
73
83
93
103
113
CUMULATIVE PERCENTAGE OF FLOWERING
NUMBER OF DAYS
FALL, 1968
POAMOHO
WAIMANALO

Figure 4. Cumulative Percentage of Flowering for the Early, Check, and Late Populations in the Two Plantings of Spring, 1969

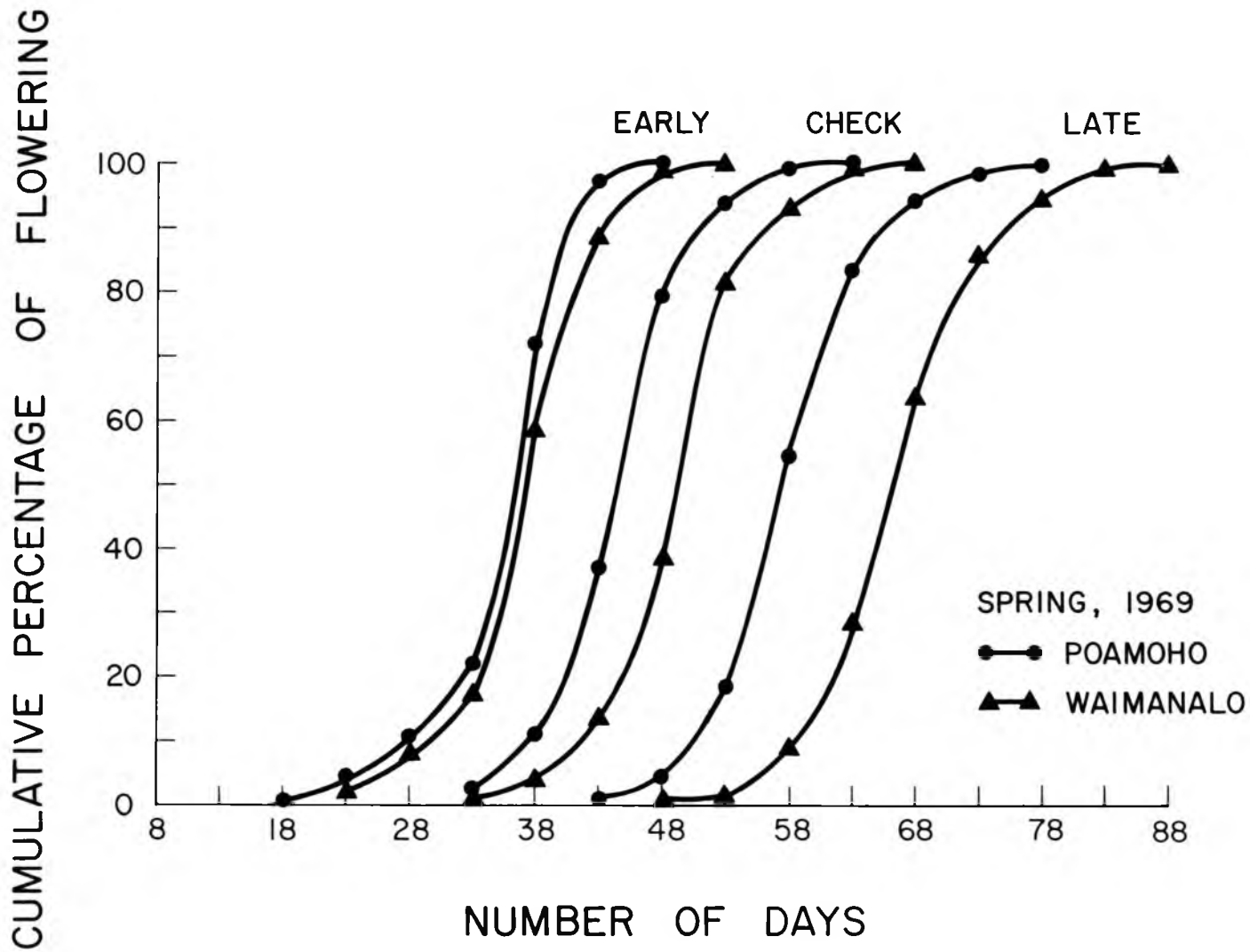

EARLY
CHECK
LATE
100
80
60
40
20
0
8
18
28
38
48
58
68
78
88
CUMULATIVE PERCENTAGE OF FLOWERING
NUMBER OF DAYS
SPRING, 1969
POAMOHO
WAIMANALO

Table 21. Realized Heritabilities of Mean Flowering Time from the Plantings Where Parents and Offspring were Grown at Same Time

Generation of Selection		Location	Season & Year	Line No.	Mean Flowering Day		Realized Heritability in Percent
Parent	Offspring				Parent	Offspring	
1st Late	2nd Late	Manoa Campus	Summer '66	25	52.54	60.33	46.06
1st Late	2nd Late	Manoa Campus	Summer '66	26	51.90	58.43	42.59
2nd Late	3rd Late	Poamoho	Spring '67	25	54.10	57.51	29.83
3rd Late	4th Late	Poamoho	Fall '67	25	69.58	76.16	38.43
3rd Late	4th Late	Greenhouse	Fall '67	25	81.06	82.00	30.22

of flowering. As a result comparisons were rather difficult to make if the parents and their offspring were in different plantings.

One of the basic assumptions for the analysis of variance is that the treatments (in this case, varieties) all have the same variances. If the treatments have significantly different variances and are, therefore, heterogeneous, then the F-test is not valid. Thus, it is important to test for heterogeneity of variances when the treatments have markedly different means. In the present studies there was a possibility of heterogeneity of variances since selection made the means of Early and Late lines more and more different. Because of this possible heterogeneity, the coefficient of variation rather than the variance was used to compare lines with different means, such as when calculating the realized heritabilities.

After four generations of selection for late flowering, two planned comparisons were made, namely the fourth generation of late selection was compared with an additional generation of late selection and with one generation of selection in opposite direction. The progeny were grown in the Summer of 1968, while the parents were grown in the Fall of 1967. Both the early and late selections bloomed in a shorter time than the parents since Radish is a long-day plant and flowers earlier in Summer than in Fall. The flowering dates of the parents were therefore transformed as described in Table 2. The results of these comparisons, using the transformed parental data, are given in Table 22. Realized heritabilities were also estimated for various groups of these same lines and are given in Table 23. Each group of lines can be traced back to a single plant.

Table 22. Effects of Selection in Opposite Direction and Continued Selection for Lateness After Four Generations of Late Selection

	4th vs. 5th Generation of Late Selection	4th Generation of Late vs. Selection in Opposite Direction
Mean Differences	5.88	4.77
Variance of Differences	22.49	32.61
St. dev. of Differences	4.74	5.71
St. Error of Differences	0.94	1.14
t - value	6.25**	4.18**

**Significant at .01 level of probability.

Table 23. Realized Heritabilities of Mean Flowering Time from the Plantings Where Parents and Offspring were Grown at Different Times

Generation of Selection		Line No.	Mean Flowering Day		Realized Heritability in Percent
Parent[a]	Offspring[b]		Parent[c]	Offspring	
4th Late	5th Late	30	63.39	70.76	46.86
4th Late	5th Late	31	64.85	70.20	34.51
4th Late	5th Late	33	63.38	66.39	31.41
4th Late	5th Late	42	61.72	66.22	33.84
4th Late	5th Late	44	59.65	62.60	20.48
4th Late	1st Early[d]	30	63.39	56.90	41.45
4th Late	1st Early	31	64.85	60.32	32.23
4th Late	1st Early	33	63.38	61.80	16.49
4th Late	1st Early	42	61.72	60.47	17.45
4th Late	1st Early	44	59.65	51.45	48.46

[a] Grown at Poamoho-Fall, 1967.
[b] Grown at Poamoho-Summer, 1968.
[c] Transformed values to make comparable with offspring. Method of transformation in Table 2.
[d] Selection in opposite direction.

The estimates of heritabilities of mean flowering time in Table 23 were obtained after eliminating part of the environmental component of variance, that due to the different planting times, from the total environmental variances. Thus these estimates may actually be biased upwards somewhat. However, the magnitude of realized heritabilities calculated in this manner was similar to the magnitude of the heritability calculated when both parents and offspring were grown at the same time (Table 21). From the results shown in Table 23 it may be concluded that the lines 33 and 42 have lost most of the genes for earliness, while line 44 has lost most of the genes for lateness. Also that lines 30 and 31 still have genes for both earliness and lateness which are not fixed. The results also show that an appreciable amount of genetic variance for flowering time is still available in these lines that have already been selected for four generations.

Main Field Experiment

The data of the four plantings at the two farms at two different times were found to be heterogeneous. The data of 10 Early, 1 Check, and 10 Late lines gave a value of 39.3 for heterogeneity Chi-square. When the lines were grouped into 3 Early, 1 Check, and 4 Late groups of lines, heterogeneity Chi-square was 28.0. Both these values are highly significant (P less than 0.01) for 3 degrees of freedom. When the data of the four plantings for 10 Early, 1 Check, and 10 Late lines were pooled and analyzed anyway, the main effects, first degree interactions, and second degree interaction were all highly significant. This was not surprising, since pooling heterogeneous data may lead to significance

even when it is not actually present. In other words, a Type I statistical error may be committed by pooling data with heterogeneous variances. In order to perform a statistically legitimate analysis, the data was transformed in the following way so that the variances were homogeneous.

The transformation used was to express all flowering dates as a percentage of a particular reference point within the individual planting. The reference point which was chosen as the most constant point from one planting to the next was the mean 100 percent flowering date of the Check lines. The reason why the mean 100 percent flowering day of the Check lines was chosen, rather than the mean 50 percent flowering day is that the frequency distribution of Check lines in the Waimanalo-Fall, 1968 planting was somewhat skewed towards earliness in flowering (Figure 3). If the 50 percent flowering day of Check lines were used, the data for this planting showed a pattern of distribution which was distinctly different from that of the other three plantings.

Mathematically the data were coded by multiplying with a particular constant, different for each of the four plantings. Statistically, such coding of data is not permissible, as it will change not only the means but also the variances. Furthermore, there is a possibility of committing a statistical error of Type II, in which the results may show nonsignificance for certain effects which are actually significant. Although it is obvious that the transformation will change the Farm and Time effects, it is assumed that it would not make any significant change in the other effects.

The transformation applied, however, is a type often used by plant breeders, who are interested in expressing the results in comparison to a certain "Check". Since it was observed in the earlier experiments that the time of planting has a great effects on the flowering time in radish, it was necessary to use a separate transformation for each individual planting. Reliance on the performance of Check lines seems appropriate on the grounds that (a) these are unselected lines and thus are probably better representatives than the selected lines of a constant level of performance; and (b) the two Check lines were identical, thus had double the accuracy than any other line in a planting.

Since the transformation was "percent of mean 100 percent flowering of Check", it may seem desirable to apply a logarithmic or arc-sin transformation to the transformed data. However, it was not necessary because the use of "percent of Check" is not causing skewness in any direction. Such a transformation might have been necessary if the data were expressed as the "percent of Late" or the "percent of Early" lines, since these might have caused skewness in the distribution.

Table 24 shows the results of analyses of variance for 10 Early and 10 Late lines for the four plantings separately. For each planting the lines effect was highly significant. The lines effect was also highly significant in the analyses of 3 Early, 1 Check and 4 Late groups of lines (Table 25).

In the analyses of variance for 1 Check and 3 Early groups of lines, the groups of lines effect was separated into two parts, viz., Early vs. Check and within Early. Table 28 shows that not only the

Table 24. Tables of Analyses of Variance for Ten Early and Ten Late Lines

Source of Variation	df	Poamoho-Fall		Poamoho-Spring		Waimanalo-Fall		Waimanalo-Spring	
		S.S.	M.S.	S.S.	M.S.	S.S.	M.S.	S.S.	M.S.
Replication	3	15.93	5.31	11.76	3.92	1.46	0.48	18.08	6.02
Lines	19	36,791.24	1,936.38**	29,351.76	1,544.82**	37,288.07	1,962.53**	43,851.14	2,307.95**
Error	57	279.87	4.91	261.26	4.58	386.47	6.78	355.86	6.24
Total	79	37,087.04	469.45	29,624.78	374.99	37,676.00	476.91	44,225.08	559.81

**Significance at .01 level of probability.

Table 25. Tables of Analyses of Variance for Three Early, One Check, and Four Late Groups of Lines

Source of Variation	df	Poamoho-Fall		Poamoho-Spring		Waimanalo-Fall		Waimanalo-Spring	
		S.S.	M.S.	S.S.	M.S.	S.S.	M.S.	S.S.	M.S.
Replication	3	12.50	4.16	0.72	0.24	4.12	1.37	5.18	1.72
Groups of Lines	7	13,296.69	1,899.52**	10,209.53	1,458.50**	13,271.85	1,895.97**	15,455.52	2,207.93**
Error	21	69.23	3.29	26.88	1.28	92.51	4.40	62.02	2.95
Total	31	13,378.42	431.56	10,237.13	330.23	13,368.48	431.24	15,522.72	500.73

**Significance at .01 level of probability.

effects due to groups of lines, but also the effects due to Early vs. Check were highly significant in all four plantings. However, within Early effects were found to be nonsignificant.

In the analyses of variance for 1 Check and 4 Late groups of lines, the groups of lines effect was also separated into two parts, vis., Late vs. Check, and within Late. The results are shown in Table 29. The groups of lines effects and Late vs. Check effects were highly significant in all four plantings. However, within Late effects were highly significant in the two plantings of Poamoho Experimental Farm, significant for the Waimanalo-Spring plantings, and nonsignificant for the Waimanalo-Fall planting.

The error variances for the four methods of comparing the Early, Check, and Late lines were tested for heterogeneity (Tables 26, 27, 30, and 31). Since the Chi-square values were nonsignificant for all of these tests, the data for the four plantings were pooled and analyzed as one combined experiment.

The combined analyses of variance for 10 Early and 10 Late lines and for 3 Early, 1 Check, and 4 Late groups of lines are given in Tables 32 and 33 respectively. In both of these combined analyses lines and the second degree interaction were highly significant. All the main effects (except lines), and the first degree interactions were nonsignificant in both the combined analyses.

The combined analysis for 1 Check and 3 Early groups of lines is given in Table 34. Here, besides lines and the second degree interaction, Farms, Early vs. Check, and within Early effects were also found to be highly significant. Only one first degree interaction, Farms x

Table 26. Test of Heterogeneity for the Four Error Variances of Ten Early and Ten Late Lines

Experiments	Error				
	df	S.S.	M.S.	log.e of M.S.	df x log.e of M.S.
Poamoho-Fall	57	279.87	4.91	1.5913	90.7041
Poamoho-Spring	57	261.26	4.58	1.5217	86.7369
Waimanalo-Fall	57	386.47	6.78	1.9140	109.0980
Waimanalo-Spring	57	355.86	6.24	1.8310	104.3670
Totals	228	1,283.46	22.51	6.8580	390.9060

Pooled M.S. = 1283/228 = 5.62

$Q = \Sigma$ df x log.e of pooled M.S. = 228 x 1.7263

= 393.5964

$$\text{Correction factor} = C = 1 + \frac{1}{3(K-1)}\left[\Sigma\left(\frac{1}{df}\right) - \frac{1}{\Sigma\ df}\right]$$

where K = number of M.S.'s being compared.

$$C = 1 + \frac{1}{9}\left[\left(\frac{4}{57}\right) - \frac{1}{228}\right] = 1.0073$$

$$X^2 = \frac{1}{C}\left[Q - \Sigma\ (\text{df x log.e of M.S.})\right] \quad \text{for K-1 df}$$

$$= \frac{1}{1.0073}\ (393.5964 - 390.9060)$$

χ^2 = 2.6079 (nonsignificant) for 3 df

Table 27. Test of Heterogeneity for the Four Error Variances of Three Early, One Check, and Four Late Groups of Lines[a]

Experiments	Error				
	df	S.S.	M.S.	log.e of M.S.	df x log.e of M.S.
Poamoho-Fall	21	69.23	3.29	1.1909	25.0089
Poamoho-Spring	21	26.88	1.28	0.2469	5.1849
Waimanalo-Fall	21	92.51	4.40	1.4816	31.1136
Waimanalo-Spring	21	62.02	2.95	1.0818	22.7178
Totals	84	250.64	11.92	4.0012	84.0252

[a]Procedure and terminology same as Table 26.

Pooled M.S. = 2.98

Q = 91.7196

C = 1.0198

Chi-square = 7.5450 (nonsignificant) for 3 df

Table 28. Tables of Analyses of Variance for One Check and Three Early Groups of Lines

Source of Variation	df	Poamoho-Fall		Poamoho-Spring		Waimanalo-Fall		Waimanalo-Spring	
		S.S.	M.S.	S.S.	M.S.	S.S.	M.S.	S.S.	M.S.
Replication	3	8.81	2.93	2.88	0.96	34.39	11.46	0.04	0.01
Groups of Lines	3	1,093.24	366.08**	638.86	212.95**	582.85	194.28	1,162.42	387.47**
Early vs. Check	(1)	(1,087.47)	(1,087.47**)	(629.23)	(629.23**)	(560.60)	(560.60**)	(1,158.27)	(1,158.27**)
Within Early	(2)	(10.77)	(5.38n.s.)	(9.63)	(4.81n.s.)	(22.25)	(11.12n.s.)	(4.15)	(2.07n.s.)
Error	9	24.73	2.74	18.71	2.07	21.49	2.38	4.84	0.53
Total	15	1,131.78	75.45	660.45	44.03	638.73	42.58	1,167.30	77.82

**Significance at .01 level of probability.
n.s.Nonsignificant.

Table 29. Tables of Analyses of Variance for One Check and Four Late Groups of Lines

Source of Variation	df	Poamoho-Fall		Poamoho-Spring		Waimanalo-Fall		Waimanalo-Spring	
		S.S.	M.S.	S.S.	M.S.	S.S.	M.S.	S.S.	M.S.
Replication	3	16.63	5.54	2.21	0.73	2.41	0.80	9.38	3.12
Groups of Lines	4	2,036.31	509.07**	1,825.19	456.29**	2,812.69	703.17**	2,460.83	615.20**
Late vs. Check	(1)	(1,938.48)	(1,938.48**)	(1,792.39)	(1,792.39**)	(2,792.83)	(2,792.83**)	(2,413.18)	(2,413.18**)
Within Late	(3)	(97.83)	(32.61**)	(32.80)	(10.93**)	(19.86)	(6.62n.s.)	(47.65)	(15.88**)
Error	12	61.62	5.13	19.23	1.60	74.40	6.20	53.43	4.45
Total	19	2,114.56	111.29	1,846.63	97.19	2,889.50	152.07	2,523.64	132.82

*Significance at .05 level of probability.
**Significance at .01 level of probability.
n.s. Nonsignificant.

Table 30. Test of Heterogeneity for the Four Error Variances of One Check and Three Early Groups of Lines[a]

Experiments	Error				
	df	S.S.	M.S.	log.e of M.S.	df x log.e of M.S.
Poamoho-Fall	9	24.73	2.74	1.0080	9.0720
Poamoho-Spring	9	18.71	2.07	0.7276	6.5484
Waimanalo-Fall	9	21.49	2.38	0.8671	7.8039
Waimanalo-Spring	9	4.84	0.53	-0.6350	-5.7150
Totals	36	69.77	7.72	1.9677	17.7093

[a]Procedure and terminology same as in Table 26.

Pooled M.S. = 1.93

Q = 23.6700

C = 1.0463

Chi-square = 5.6969 (nonsignificant) for 3 df

Table 31. Test of Heterogeneity for the Four Error Variances of One Check and Four Late Groups of Lines[a]

Experiments	Error				
	df	S.S.	M.S.	log.e of M.S.	df x log.e of M.S.
Poamoho-Fall	12	61.62	5.13	1.6351	19.6212
Poamoho-Spring	12	19.23	1.60	0.4700	5.6400
Waimanalo-Fall	12	74.40	6.20	1.8246	21.8952
Waimanalo-Spring	12	53.43	4.45	1.4929	17.9148
Totals	48	208.68	17.38	5.4226	65.0712

[a]Procedure and terminology same as in Table 26.

Pooled M.S. = 4.34

Q = 70.4592

C = 1.0347

Chi-Square = 5.2073 (nonsignificant) for 3 df

Table 32. Combined Analyses of Variance for Ten Early and Ten Late Lines

Source of Variation	df	S.S.	M.S.
Farms (F)	1	87.09	87.09$^{n.s.}$
Time (T)	1	15.31	15.31$^{n.s.}$
F x T	1	10.23	10.23$^{n.s.}$
Error (a)	12	47.24	3.93
Reps. over Experiments	15	159.87	10.65
Lines (B)	19	146,133.51	7,691.23**
B x F	19	467.07	24.58$^{n.s.}$
B x T	19	293.80	15.46$^{n.s.}$
B x F x T	19	387.83	20.41**
Error (b)	228	1,283.44	5.62
Total	319	148,725.52	466.22

$^{n.s.}$Nonsignificant.
**Significant at .01 level of probability.

F-tests:

Farms	has been tested against B x F
Time	has been tested against B x T
F x T	has been tested against Error (a)
B	has been tested by an indirect test (refer Table 14)
B x F	has been tested against B x F x T
B x T	has been tested against B x F x T
B x F x T	has been tested against Error (b)

Table 33. Combined Analyses of Variance for Three Early, One Check, and Four Late Groups of Lines

Source of Variation	df	S.S.	M.S.
Farms (F)	1	28.37	28.37$^{n.s.}$
Time (T)	1	2.12	2.12$^{n.s.}$
F x T	1	7.77	7.77$^{n.s.}$
Error (a)	12	22.52	1.87
Reps. over Experiments	15	60.78	4.05
Lines (B)	7	51,845.68	7,406.52**
B x F	7	170.86	24.40$^{n.s.}$
B x T	7	31.46	4.49$^{n.s.}$
B x F x T	7	185.59	26.51**
Error (b)	84	250.63	2.98
Total	127	52,545.00	413.74

$^{n.s.}$Nonsignificant.
**Significant at .01 level of probability.

F - tests same as in Table 32.

Table 34. Combined Analyses of Variance for One Check and Three Early Groups of Lines

Source of Variation	df	S.S.	M.S.
Farms (F)	1	23.10	23.10**
Time (T)	1	8.92	8.92n.s.
F x T	1	22.98	22.98*
Error (a)	12	46.12	3.84
Reps. over Experiments	15	101.12	6.74
Lines (B)	3	3,392.82	1,130.94**
Early vs. Check	(1)	(3,350.77)	(3,350.77**)
Within early	(2)	(42.05)	(21.02**)
B x F	3	0.69	0.23n.s.
B x T	3	4.24	1.41n.s.
B x F x T	3	84.62	28.20**
Error (b)	36	69.76	1.93
Total	63	3,653.25	57.98

n.s. Nonsignificant.
* Significance at .05 level of probability.
** Significance at .01 level of probability.

F - tests same as in Table 32.

Times, was significant. Although the within Early effect was non-significant in all the four individual analyses of variance, it was found to be highly significant in the combined analysis. This might be due to the fact that the means of the three Early groups of lines had slight, nonsignificant differences and occurred in the same sequence in all four plantings. In the combined analysis these small, constant differences evidently became highly significant. The mean flowering time was earliest in the first group of lines, slightly later in the second group, and latest in the third group. The pedigrees show that these three groups of lines had previously been selected for late flowering for 0, 1, and 2 generations. These results show that in spite of the great influence of environment on the time of flowering, selection was effective.

Table 35 shows the results of the combined analysis of variance for 1 Check and 4 Late groups of lines. Among the main effects Lines and Late vs. Check were highly significant, while among the interactions Farms x Times and Lines x Farms were highly significant and significant, respectively. Although significance was observed for the within Late effect in three out of the four plantings, in the combined analysis this effect was nonsignificant. This probably was due to inconsistency in the ranking of the four groups of lines in different plantings. The results suggest that the original four seeds, from which the four groups of Late lines were developed, were probably not different genetically from each other and that the response to selection in these groups of lines was probably also alike.

Table 35. Combined Analysis of Variance for One Check and Four Late Groups of Lines

Source of Variation	df	S.S.	M.S.
Farms (F)	1	97.88	97.88$^{n.s.}$
Time (T)	1	0.09	0.09$^{n.s.}$
F x T	1	105.64	105.64**
Error (a)	12	30.63	2.55
Reps. over Experiments	15	234.24	15.61
Lines (B)	4	9,013.62	2,253.40**
Late vs. Check	(1)	(8,867.62)	(8,867.62**)
Within Late	(3)	(146.00)	(48.66$^{n.s.}$)
B x F	4	84.09	21.02*
B x T	4	26.88	6.72$^{n.s.}$
B x F x T	4	10.43	2.60$^{n.s.}$
Error (b)	48	208.67	4.34
Total	79	9,577.93	121.23

$^{n.s.}$Nonsignificant.
*Significant at .05 level of probability.
**Significant at .01 level of probability.

F - tests same as in Table 32.

The variance components obtained from the combined analyses are given in Table 36. This table shows the magnitude of the variance components in four different types of analyses. From this table it seems probable that the cause of the second degree interaction component is in the Early lines. Furthermore, this table shows that the behavior of the Early and Late lines is quite different. Some of the effects that are significant in one are nonsignificant in the other and vice versa. When the Early and Late "populations" were grouped, they nullified some of the significant effects of each other.

The Farms and Times effects were nonsignificant in the four combined analyses, although from the raw data (Tables 4 to 7), it seems that these effects should be significant. This, of course, is due to expressing the data relative to the performance of the Checks. Two planned comparisons to check the significance of Farms and Times were made with the non-transformed data. The results, given in Table 37, show that both the effects were highly significant in all the four types of grouping of the lines.

In Figures 3 and 4, Early, Check, and Late represent the means of all the Early, Check and Late lines respectively. Figure 4 shows gradually increasing differences between the two Farms from Early to Check, and from Check to Late. However, the data of Fall, 1968 (Figure 3) shows that the differences between the two farms remained fairly uniform.

Figures 5 and 6 are constructed directly from Figures 3 and 4 respectively. The ordinates of these figures give the cumulative percentages of flowering time of the Early and Late lines expressed as

Table 36. Variance Component Estimates from Combined Analyses of Variance

Variance Components[a]	10 Early & 10 Late Lines	3 Early, 1 Check & 4 Late Groups of Lines	1 Check & 3 Early Groups of Lines	1 Check & 4 Late Groups of Lines
σ^2_{BFT}	3.6975**	5.8825**	6.5675**	0.0000[b]
σ^2_{BT}	0.0000[b]	0.0000[b]	0.0000[b]	0.5150[n.s.]
σ^2_{BF}	0.5212[n.s.]	0.0000[b]	0.0000[b]	2.3025*
σ^2_{B}	479.5318**	461.3200**	68.8018**	140.7868**
σ^2_{FT}	0.0000[b]	0.0000[b]	0.0000[b]	5.2415**
σ^2_{T}	0.0626[n.s.]	0.2557[n.s.]	0.3978[n.s.]	0.0000[b]
σ^2_{F}	0.4543[n.s.]	0.3548[n.s.]	0.8849**	0.0000[b]
σ^2	5.6200	2.9800	1.9300	4.3400

[a]For description see Table 11.
[b]Negative estimates for which the most reasonable value is zero.
n.s. Nonsignificant.
*Significant at .05 level of probability.
**Significant at .01 level of probability.

Table 37. Effects of Location and Planting Time on Flowering

	10 Early & 10 Late Lines	3 Early, 1 Check & 4 Late Groups of Lines	1 Check & 3 Early Groups of Lines	1 Check & 4 Late Groups of Lines
Location:				
Mean differences	5.91	5.89	3.44	7.42
Variance of differences	7.38	7.24	0.04	4.92
St. dev. of differences	2.72	2.69	0.20	2.22
St. Error of differences	0.61	0.95	0.10	0.99
t-Value	9.85**	6.20**	34.40**	7.49**
Planting Time:				
Mean differences	17.45	18.06	13.72	21.08
Variance of differences	23.58	22.90	2.15	9.49
St. dev. of differences	4.86	4.79	1.47	3.08
St. Error of differences	1.08	1.69	0.73	1.37
t-Value	16.15**	10.68**	18.79**	15.38**

**Significance at .01 level of probability.

Figure 5. Deviations from the Check of Cumulative Percentages of Flowering for the Early, Check and Late Populations in the Two Plantings of Fall, 1968

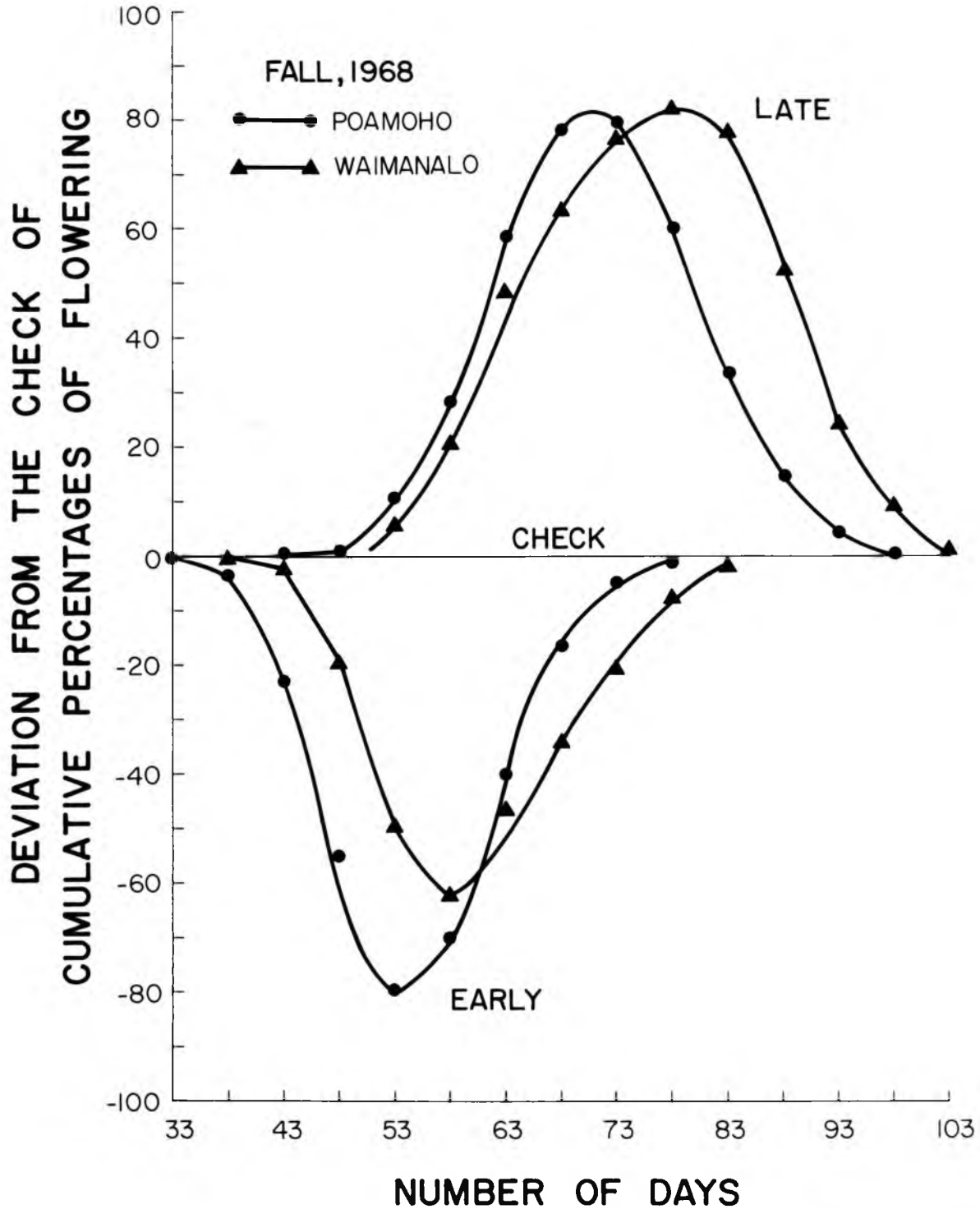
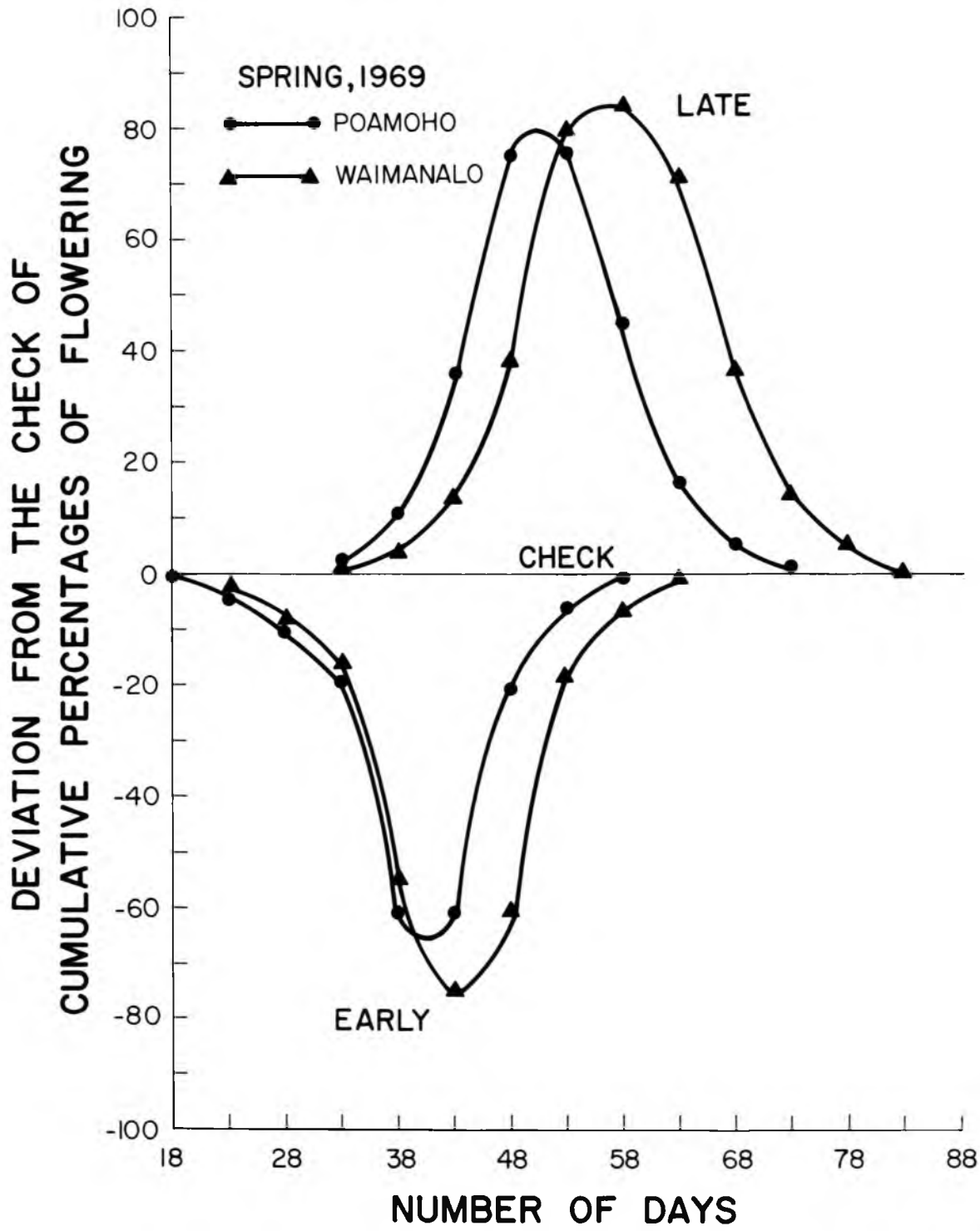

FALL, 1968
POAMOHO
WAIMANALO
LATE
CHECK
EARLY
DEVIATION FROM THE CHECK OF CUMULATIVE PERCENTAGES OF FLOWERING
NUMBER OF DAYS
100
80
60
40
20
0
-20
-40
-60
-80
-100
33
43
53
63
73
83
93
103

Figure 6. Deviations from the Check of Cumulative Percentages of Flowering for the Early, Check, and Late Populations in the Two Plantings of Spring, 1969


SPRING, 1969
POAMOHO
WAIMANALO
LATE
CHECK
EARLY
DEVIATION FROM THE CHECK OF CUMULATIVE PERCENTAGES OF FLOWERING
NUMBER OF DAYS
100
80
60
40
20
0
-20
-40
-60
-80
-100
18
28
38
48
58
68
78
88

deviations from the Check for the respective classes on the abscissa. At the earliest dates flowering had started in the Early lines, while there was no flowering in the Check. Thus to get the deviations from the Check (ordinate values) a value of zero was given to the Check. Similarly, at the latest dates flowering had finished in the Check lines, while the Late lines were still blooming. Thus to get the deviations from the Check a value of 100 was given to the Check. These Figures show that the maximum cumulative difference of the Late lines from the Check lines was the same in the two plantings of Fall, 1968. This reflects the similar performance of the Late population in the two plantings of Fall, 1968. Similarly, the maximum cumulative differences of the Late lines from the Check lines are not very different in the two plantings of Spring, 1969. Furthermore, in the Late populations the relation between Poamoho and Waimanalo plantings of Fall, 1968 is very similar to the relation between the Poamoho and Waimanalo plantings of Spring, 1969. The maximum cumulative differences of the Early lines from the Check lines are quite different in the two plantings of Fall, 1968 (Figure 5). This shows that the performance of the Early populations in the two plantings was different. The differences are also noted in the two plantings of Spring, 1969 (Figure 6). It can also be noted that while the maximum deviation of Early lines from the Check was higher in Poamoho in the Fall, 1968 plantings, the maximum deviation was higher in Waimanalo, for the Spring, 1969 plantings. These discrepencies noted in the Early lines, particularly in 1968, and not in the Late lines explain the significant second degree interaction

for the Early population, and the nonsignificant interaction for the Late population (Table 36).

Estimates of the heritability of the mean flowering time of the Check line were made, assuming that (a) lines L-2, L-3, L-6, L-7, and L-10 are homozygous, and thus the variance of flowering time in these lines is a valid estimate of the environmental variance, and (b) the variation due to the environment of the Check line is of the same magnitude as that of the Late lines in a particular planting. The estimates obtained from the Waimanalo-Fall planting were considerably higher than those of the other plantings (Table 38). The reason for this is the skewed distribution of the Check line in that planting. The skewed distribution yielded considerably higher variance of the Check lines in this planting (Table 17). The higher variance of the Check line is expected to give higher estimates of heritability.

The variance due to the breeding lines was not used as an estimate of the total genetic variance, because the breeding lines had been selected in opposite directions and thus had a higher variance than would be expected from unselected families or from an F_2 population. A heritability estimate calculated from this variance would be expected to have a high positive bias when the breeding lines had been selected in opposite directions.

Crossing Experiments

The means, variances, standard deviations, and coefficients of variations of flowering time in P_1, P_2, F_1, and F_2 are given in Table 40. The estimates of heritabilities of flowering time, calculated from the

Table 38. Estimates of Heritabilities of Mean Flowering Time of Check Line, Considering L-2, L-3, L-6, L-7, and L-10 as Homozygous Lines

Homozygous Lines	Poamoho		Waimanalo	
	Fall	Spring	Fall	Spring
L-2	21.41	32.29	28.58	30.78
L-3	33.31	46.83	63.79	40.09
L-6	46.79	41.81	69.79	41.98
L-7	38.05	31.34	64.07	29.30
L-10	47.86	32.88	67.54	30.19

variances of F_1 and F_2 are also given in this table. The average heritability of flowering time in the F_2 was found to be 34.90 percent. The frequency distributions of P_1, P_2, F_1, and F_2 are given in Figure 7.

The F_1 was grown in two replications and included all reciprocal crosses as well. The effects of these two factors are given in Table 39. The effect of the replications was highly significant, most likely due to the effect of the two different sizes of cans used for the two replications. There were no significant differences in the mean flowering time between reciprocal crosses, therefore, these were combined for all subsequent analyses. Two comparisons, described in Table 39, were made from the data given in Table 20, which gives the mean flowering day of the F_1 plants that had either a male common parent or a female common parent.

The variances as well as the coefficients of variation were much lower in P_1 and P_2 than in the F_1 generation. The reason for this is that the parental plants used for the crosses do not represent the full range of blooming dates for the parental lines. There was a deliberate selection of plants that bloomed more or less at the same time to constitute each parental group. This was true for both parents in both sets. For this reason, the estimation of environmental variance was based only on the F_1 data, rather than the mean of P_1, P_2, and F_1 data. The results of the crossing experiments show no dominance for the time of flowering, and are not in accordance with the results of a previous worker (Frost, 1923). He has reported contradictory results from the crosses of early and late lines of Raphanus sativus and R. raphanistrum. From the one set of experiments he concluded that the

Figure 7. Frequency Distributions of Days to Flowering in P_1, P_2, F_1 and F_2

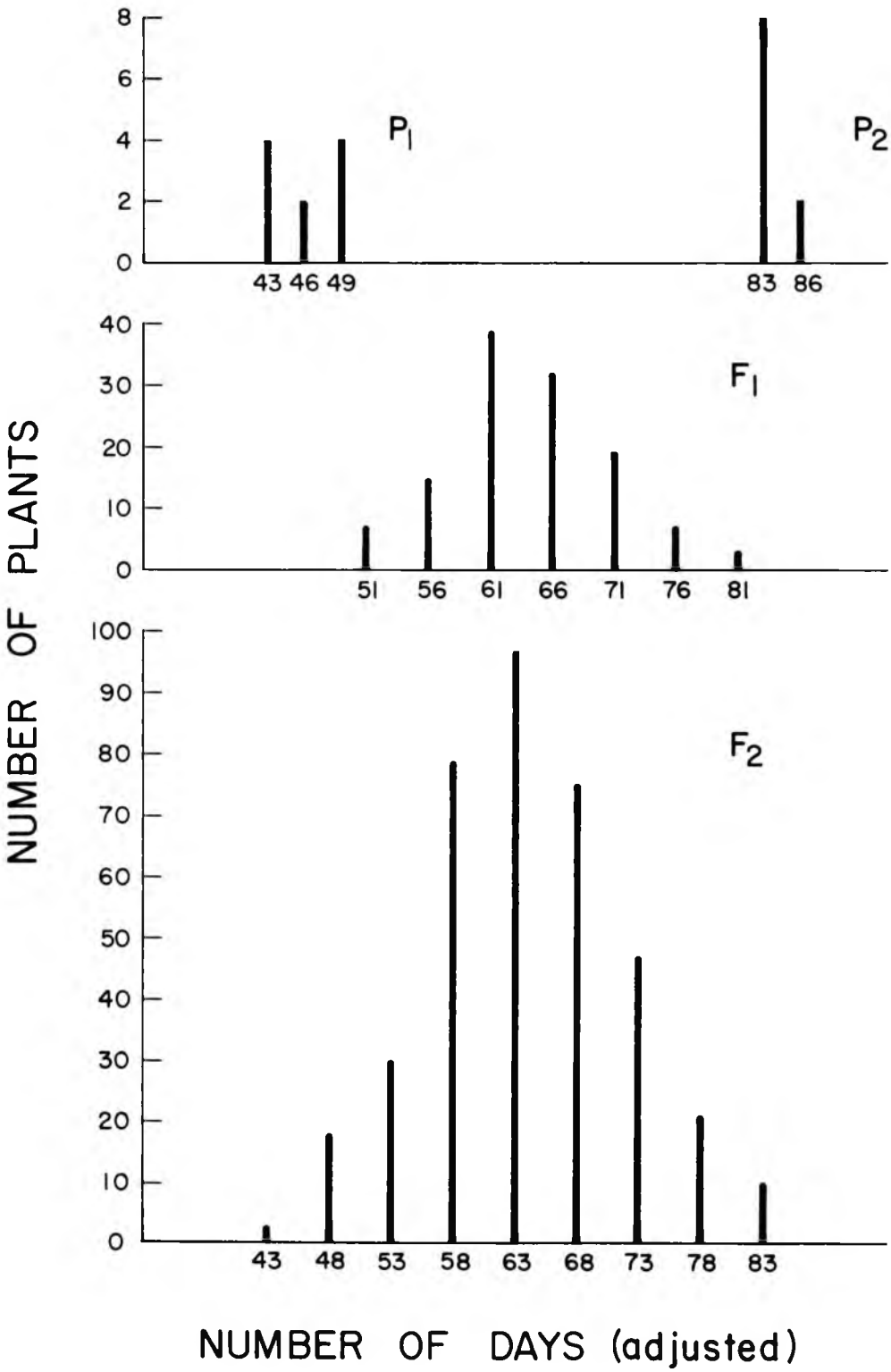

NUMBER OF PLANTS
P1
P2
F1
F2
43 46 49
83 86
51 56 61 66 71 76 81
43 48 53 58 63 68 73 78 83
NUMBER OF DAYS (adjusted)

Table 39. Effects of Replication and Reciprocal Crosses on Mean Flowering Day of F_1 Progeny

	Rep. I vs. Rep. II	Crosses vs. Reciprocal Crosses
Mean differences	1.97	1.42
Variance of differences	6.02	26.82
St. dev. of differences	2.45	5.18
St. Error of differences	0.55	1.16
t-Value	3.58^{**}	$1.23^{n.s.}$

$^{n.s.}$Nonsignificant.
**Significant at .01 level of probability.

Table 40. Mean, Variance, Standard Deviation, and Coefficient of Variation of Flowering Time in P_1, P_2, F_1 and F_2; and Estimation of Heritability

	Set I	Set II	Combined
P_1:			
n	5	5	10
Mean	44.20	47.80	46.00
Variance	4.70	5.20	8.00
St. deviation	2.17	2.28	2.83
C.V. (%)	4.90	4.76	6.15
P_2:			
n	5	5	10
Mean	84.00	83.80	83.90
Variance	3.00	1.70	2.10
St. deviation	1.73	1.30	1.45
C.V. (%)	2.05	1.55	1.72
F_1:[a]			
n	61	61	122
Mean	62.83	64.93	63.88
Variance	41.93	42.22	42.84
St. deviation	6.48	6.50	6.55
C.V. (%)	10.31	10.01	10.25
F_2:[a]			
n	193	187	380
Mean	64.70	63.09	63.91
Variance	62.00	68.77	65.81
St. deviation	7.88	8.29	8.11
C.V. (%)	12.17	13.13	12.68
Heritability (%)	32.37	38.60	34.90

[a]Transformed data.

time of flowering in radish is controlled by a "recessive lateness gene", while the results of another planting reported in the same study showed it to be controlled by a "dominant lateness gene". Probably the contradictory results were due to the lack of a proper control in his plantings. However, the results of the present study are in accordance to those reported by Panetsos and Baker (1968). They found the hybrids of two species of radish to be almost intermediate between the parents in the duration of the period from germination to flowering.

The F_2 distribution (Figure 7) shows that there are probably many genes responsible for the time of flowering, though it seems rather difficult to make an estimation of the actual number of genes involved. Even though about 1/16 of the F_2 are equal to the parent, it seems likely that more than 2 pairs of genes are involved, since the response to selection was gradual, and an appreciable amount of variation was found even after six generations of selection. Panetsos and Baker (1968) have also concluded that flowering time in radish is polygenically controlled, though they recognized three distinct groups, with the ratios of 5 : 10 : 3 in the F_2 generation. Growing all generations under controlled conditions for environmental factors such as photoperiod, light intensity, temperature, etc. may very likely lead to a reliable estimate of the number of genes responsible for the time of flowering in radish.

Since the estimates of heritability of flowering time obtained by the three methods described in the Selection Experiment, Main Field Experiment, and Crossing Experiments were quite similar, it was concluded that the three methods seem equally reliable.

SUMMARY AND CONCLUSIONS

The genetics of flowering time in Raphanus sativus L. cv. 'Chinese Daikon' was studied in three phases, a) bidirectional selection studies, b) studies to estimate genotype-environment interactions, and c) crossing studies with Early and Late selected lines.

Individual plant selection, from the original open-pollinated parent, was practiced for six generations for late flowering, and for four generations for early flowering. Realized heritabilities of mean flowering time were computed using the formula for genetic advance, $G_S = k \times \text{St. dev.} \times h^2$. The average realized heritability in the first four generations of selection was 37.42 percent. The assumptions on which these estimations were based and the limitations of the results are described and discussed. The estimation of realized heritability in the more advanced generations was somewhat lower, about 33 percent. From the results of selection in the opposite direction it was concluded that an appreciable amount of genetic variability was present even after 4 generations of selection. Since planting time had a great effect on the mean flowering day, transformation of data was necessary to make comparisons between plantings at different times. The assumptions for such a transformation are discussed.

To study the genotype-environment interaction, 10 Early, 2 Check, and 10 Late lines were grown in a Randomized Complete Block Design at two locations during two times of year. Data on 50 percent flowering time were found to be significantly heterogeneous for the four plantings. However, the data became homogeneous after transformation based on the performance of Check lines in the individual plantings. The effects of

the transformation are described and the justification for such a transformation is discussed. Breeding lines were grouped, based on their pedigrees, in four different ways. Analyses of variance of transformed data were done for each type of grouping, separately for the individual plantings as well as combined for all four plantings.

The magnitudes of the various variance components were quite different for Early and Late lines. The combined analyses of variance for Early and Late lines nullified some effects that were significant in the separate analyses. An attempt has been made to identify the possible causes of significance of the various effects.

Estimations of the heritability of mean flowering time of the Check line were possible after certain assumptions on the causes of variability in the selected lines were made. The estimation from the data of three of the plantings were similar to those obtained from the selection experiments. The skewed distribution of the flowering time of the Check lines in the fourth planting was postulated to be the cause of the somewhat higher values of heritability from that planting.

Crossing experiments between Early and Late lines were conducted in the greenhouse. For this purpose, 10 Early, and 10 Late plants were divided into two sets (each set consisting of 5 early and 5 late plants). The crosses were made between Early and Late plants in all the possible combinations (including reciprocals) within each set. No significant differences between the crosses and their reciprocals were found for the time of flowering. The data of both the F_1 and F_2 plantings were adjusted by comparing with check plants to make the data of these plantings comparable to that of the original parental planting.

Frequency distributions of the F_1 and F_2 showed no dominance for the time of flowering and indicated that there probably are many genes controlling this character. The heritability for the time of flowering was 34.90 percent as calculated from the variances of F_1 and F_2 generations.

LITERATURE CITED

Abegg, F. A. 1936. A genetic factor for the annual habit in beets and linkage relationship. J. Agr. Res. 53:493-511.

Allard, H. A. 1919. Gigantism in Nicotiana tabacum and its alternative inheritance. Amer. Nat. 53:218-233.

Allard, R. W. 1956. The analysis of genetic-environmental interactions by means of diallel crosses. Genetics 41:305-318.

Allard, R. W. and A. D. Bradshaw. 1964. Implications of genotype-environmental interactions in applied plant breeding. Crop Sci. 4:503-508.

Banga, O. and J. L. Van Bennekom. 1962. Breeding radish for winter production under glass. Euphytica 11:311-326.

Banga, O. and L. Smeets. 1956. Some effects of the photoperiod on growth and pithiness of radishes. Euphytica 5:196-204.

Bremer, A. H. 1931. Einfluss der Tageslange auf die Wachstumsphasen des Salats. Genetische Untersuchungen I. Gartenbauwiss. 4:469-483.

Bremer, A. H. and J. Grana. 1935. Genetische Untersuchungen mit Salat II. Gartenbauwiss. 9:231.

Charles, D. R. and H. H. Smith. 1939. Distinguishing between two types of gene action in quantitative inheritance. Genetics 24:34-38.

Cochran, W. G. and G. M. Cox. 1955. Experimental designs. 2nd. Ed. John Wiley, New York. 611 pp.

Collier, W. L., J. R. Davidson and T. Pee. 1967. Analysis of Daikon production on the Island of Hawaii. Agricultural Economics Report No. 75. Hawaii Agr. Exp. Sta. pp. 15.

Coyne, D. P. 1966. The genetics of photoperiodism and the effect of the photoperiodic response for time of flowering in Phaseolus vulgaris L. Proc. Amer. Soc. Hort. Sci. 89:350-360.

da Silva, W. J. and J. H. Lonnquist. 1968. Genetic variances in populations developed from full sib and S_1 testcross progeny selection in an open-pollinated variety of Maize. Crop Sci. 8:201-204.

Davies, D. R. 1959. Studies of flowering time and morphology in dwarf barley. Genetica 30:233-239.

Dickerson, G. E. and J. C. Grimes. 1947. Effectiveness of selection for efficiency of gain in Duroc swine. J. An. Sci. 6:265-287.

Dudok van Heel, J. P. 1927. Inheritance of bolting in sugarbeet. Genetica 9:217-236.

Eguchi, T., T. Matsumura and T. Koyama. 1963. The effect of low temperature on flower and seed formation in Japanese radish and Chinese cabbage. Proc. Amer. Soc. Hort. Sci. 82:322-331.

Eunus, A. M. and M. A. Salam. 1969. Epistasis in the inheritance of quantitative characters in jute. Crop Sci. 9:167-169.

Falconer, D. S. 1953. Selection for large and small size in mice. J. Genet. 51:470-501.

Falconer, D. S. 1955. Patterns of response in selection experiments with mice. Cold Spring Harb. Symp. Quant. Biol. 20:178-196.

Fisher, R. A. 1918. The correlations among relatives on the supposition of Mendelian inheritance. Trans. Royal Soc. of Edinburgh. 52:399-433.

Frost, H. B. 1923. Heterosis and dominance of size factors in Raphanus. Genetics 8:116-153.

Garner, W. W. and H. A. Allard. 1920. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. J. Agr. Res. 18:553-606.

Garner, W. W. and H. A. Allard. 1923. Further studies in photoperiodism, the response of day and night. J. Agr. Res. 23:871-877.

Goodman, M. M. 1965. Estimates of genetic variance in adapted and exotic populations of Maize. Crop Sci. 5:87-90.

Goodwin, R. A. 1944. The inheritance of flowering time in a short day species, Solidago sempervirens L. Genetics 29:503-519.

Hallauer, A. R. 1965. Inheritance of flowering in Maize. Genetics 52:129-137.

Hardin, R. T. and A. E. Bell. 1967. Two-way selection for body weight in Tribolium on two levels of nutrition. Gent. Res., Camb. 9:309-330.

Hill, J. 1965. Environmental induction of heritable changes in Nicotiana rustica. Nature 207:732-734.

Hill, J. 1967. The environmental induction of heritable changes in Nicotiana rustica parental and selection lines. Genetics 55:735-754.

Hill, J. and J. M. Perkins. 1969. The environmental induction of heritable changes in Nicotiana rustica. Effects of genotype-environment interactions. Genetics 61:661-675.

Honma, S., S. H. Wittwer and S. C. Phatak. 1963. Flowering and earliness in the tomato. J. Hered. 54:212-218.

Jinks, J. L. 1954. The analysis of continuous variation in a diallel cross of Nicotiana rustica varieties. Genetics 39:767-788.

Jinks, J. L. 1956. The F_2 and backcross generations from a set of diallel crosses. Heredity 10:1-30.

Kohel, R. J., C. F. Lewis and T. R. Richmond. 1965. The genetics of flowering response in cotton. V. Fruiting behavior of Gossypium hirsutum and Gossypium barbadense in interspecific hybrids. Genetics 51:601-604.

Krider, J. L., B. W. Fairbanks, W. E. Carroll and E. Roberts. 1946. Effectiveness of selecting for rapid and for slow growth rate in Hampshire swine. J. An. Sci. 5:3-15.

Krjuckov, A. V. 1963. The use of certain environmental conditions in the selection of radishes resistance to the tendency to bolting. (Russian) Dokl. mosk. sel'.-hoz. Akad. K. A. Timirjazeva. 83:235-240. in Hort. Abst. 34:714.

Lang, A. 1948. Beitrage zur Genetik des Photoperiodismus. I. Faktorenanalyses des Kurztagcharacter von Nicotiana tabacum Maryland Mammut. Nachtrag: Genetik der Vernalisation und des Photoperiodismus, pp. 175-189. In A. E. Murneek and R. O. Whyte (Editors): Vernalization and photoperiodism. Waltham, Mass.: Chronica Botanica.

Lang, E. R. 1961. Predicted and actual responses during long-term selection for chemical composition in Maize. Eyphytica 10:368-378.

Lang, E. R. 1962. Selection reversal in strains of corn previously long-term selected for chemical composition. Crop Sci. 2:167-170.

Liang, G. H. L. and T. L. Walter. 1968. Heritability estimates and gene effects for Agronomic traits in grain sorghum, Sorghum vulgare pers. Crop Sci. 8:77-81.

Lindqvist, K. 1960. Inheritance studies in lettuce. Hereditas 46:387-470.

Lindsey, M. F., J. H. Lonnquist and C. O. Gardner. 1962. Estimates of genetic variance in open-pollinated varieties of Cornbelt corn. Crop Sci. 2:105-108.

Owen, F. V., E. Carsner and M. Stout. 1940. Photothermal inducation of flowering in sugar beets. J. Agr. Res. 61:101-124.

Panetsos, C. A. and H. G. Baker. 1968. The origin of variation in "wild" Raphanus sativus (Cruciferae) in California. Genetics 38:243-274.

Parlevliet, J. E. 1968. Breeding for earliness in spinach (Spinacia oleracea L.) as based on environmental and genetic factors. Euphytica 17:21-27.

Perkins, J. M. and J. L. Jinks. 1968a. Environmental and genotype-environmental components of variability. III. Multiple lines and crosses. Heredity 23:339-356.

Perkins, J. M. and J. L. Jinks. 1968b. Environmental and genotype-environmental components of variability. IV. Non-linear interaction for multiple inbred lines. Heredity 23:525-535.

Powers, LeRoy. 1942. The nature of the series of environmental variances and the estimation of genetic variacnes and the geometric means of crosses involving species of Lycopersicon. Genetics 27:561-575.

Prevosti, A. 1967. Inversion heterozygosity and selection for wing length in Drosophila subobscura. Gent. Res., Camb. 10:81-93.

Quinby, J. R. 1966. Fourth maturity gene locus in Sorghum. Crop Sci. 6:516-518.

Robertson, F. W. 1955. Selection response and the properties of genetic variation. Cold Spring Harb. Symp. Quant. Biol. 20:166-177.

Robinson, H. F., R. E. Comstock and P. H. Harvey. 1949. Estimates of heritability and the degree of dominance in corn. Agron. J. 41:353-359.

Rowlands, D. G. 1964. Genetic control in Pisum sativum L. Genetica 35:75-94.

Sinskaja, E. 1962. On the nature and conditions of the formation of esculent roots. Bull. Appl. Bot. and Pl. Br. 16:26-35.

Smith, H. H. 1950. Differential photoperiod response from an interspecific gene transfer. J. Hered. 41:199-203.

Sulgin, I. A. 1964. On the effect of visible and infra-red radiation on the development of radishes. (Russian) Fiziol. Rast. 11:398-408. in Hort. Abst. 34:714.

Sutton, E. P. F. 1924. Inheritance of "Bolting" in cabbage. J. Hered. 15:257-260.

Warner, J. N. 1952. A method for estimating heritability. Agron. J. 44:427-430.

Woodworth, C. M., E. R. Leng and R. W. Jugenheimer. 1952. Fifty generations of selection for protein and oil in corn. Agron. J. 44:60-65.

Zimmerman, L. H. 1957. Complementary genes for bloom in Ricinus communis L. J. Hered. 48:242-243.

Zucker, L. M. 1960. Model breeding experiment for two-way selection in small populations showing directional dominance. Genetics 45:485-498.